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The use of landscape features and habitats by the lesser horseshoe bat (*Rhinolophus hipposideros*)

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A dissertation submitted to the University of Bristol in accordance with the requirements of the degree of PhD in the Faculty of Science

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Abstract

This study examines the diet and foraging behaviour of *Rhinolophus hipposideros* from maternity colonies in three contrasting landscapes within Britain. Geographical and seasonal variations in diet and habitat selection exist. Broad-leaved woodlands, water, rural settlements and pastures with wooded edge or unmanaged hedges were generally most utilised and broad-leaved tree cover and edge habitats are likely to be of key importance. The presence of non-volant prey in the diet confirms gleaning, but the majority of prey is probably caught on the wing during aerial hawking, within or close to the tree canopy. Feeding on swarming insects may play a major part in foraging, with dusk, and to a lesser extent dawn, being important foraging times. The first flying bout was significantly longer in the lowland implying feeding is more efficient in the high quality and upland landscapes. Bats flew for on average 57 % of the night but colder temperatures and increasing rainfall resulted in bats flying for longer. They may aim to reach a target of energy consumption, which takes longer in poorer conditions. An average of 2.1–4.5 night roosting bouts were recorded and *R. hipposideros* may deviate from the more typical bimodal pattern as their broad diet allows them to feed throughout the night. Night roosts were significantly nearer to core foraging areas than the maternity roost and may form an integral part of the core areas. Foraging density was estimated to be 0.09-0.50 bats/ha. The ranging behaviour was consistent across the three landscapes. Average home range was 147-177 ha and mean maximum distance from the maternity roost was 2 km. It is likely that the bats were adopting an optimal behaviour that is constrained by the species' morphology. The implications of the findings for the species' conservation are discussed and management recommendations are made.

This work is dedicated to my Dad, to Dave Clarke
and to my husband John.

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Author's Declaration

This thesis is the result of my own original work, except where due acknowledgement has been made. I carried out all of the field work, including the radio-telemetry, and the faecal analysis. The literature reseach, writing, data analyses and conclusions contained in this thesis are entirely the result of my own work. No part of this work has been submitted in any previous application for a higher degree. The views expressed in this thesis are my own and not those of the University.

Tessa Knight Knight **Date** 12.10.2006

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CHAPTER ONE

INTRODUCTION

1 Introduction

This study aims to examine several aspects of the foraging ecology of the vulnerable temperate bat species *Rhinolophus hipposideros* (Bechstein, 1800) and place the findings in context of their implications for its conservation. In this introduction I provide background details on the study species, and review the current understanding of its foraging ecology. The current criteria for the conservation of bats in Britain are described, with particular emphasis on the study species. Finally the main aims of this study are summarised, and the thesis organisation outlined.

1.1 *Status and distribution*

There are 69 species of the family Rhinolophidae worldwide, covering Europe, Africa, Asia and Australasia, although the majority are confined to the tropics of Africa and Asia (Nowak 1994). Five species are native to Europe but only two: the lesser horseshoe bat *R. hipposideros* and the greater horseshoe bat *Rhinolophus ferrumequinum* are present in Britain. *R. hipposideros* is found from south-west Europe and north-west Africa, east to the Himalayas. It is at the northern limit of its distribution in Britain, where it has undergone a contraction in range in the past hundred years (Mitchell-Jones 1994-1995). It is currently widely distributed in Wales but confined to south-west England as far east as Dorset, Oxfordshire and Warwickshire (Richardson 2000). It appears to have disappeared from Durham, the Peak District, Northumberland and North Yorkshire (Macdonald and Tattersall 2001). There are also early records as far east as Norfolk and Kent and subfossils of the species have been found as far north as Derbyshire (Yalden 1999). In Europe populations of *R. hipposideros* declined rapidly from the 1950s and 1960s throughout the Netherlands, Belgium, Germany, Switzerland and Poland and now the species is virtually extinct in large areas of north-west Europe (Stebbings 1988). The species is classified as Endangered in Britain and Europe (Hutson 1993, Harris et al. 1995) and as Vulnerable (code VU A2c) to extinction by the International Union of Conservation for Nature and Natural Resources (IUCN) (Hutson et al. 2001).

The British and Irish populations are significant numerically in a European context (Ohlendorf 1997) and now form one of the European strongholds (Macdonald and Tattersall 2001). Although there are no estimates for its worldwide population, recent population estimates within Britain suggest the population is increasing. They range from 14,000 individuals, split equally between England and Wales (Harris et al. 1995) to 17,000 individuals with 7,000 present in England and 10,000 present in Wales (Altringham 2003), with 18,000 individuals estimated in 2005 (Battersby 2005). The National Bat Monitoring Programme has recorded a significant upward trend from the survey of hibernation sites (Bat Conservation Trust 2004). The trend shows a significant increase of 45.2 % between 1997 and 2004, with an annual increase estimated at 7.74 %. The trend from the summer colony counts also shows a significant increase of 44.4 % between 1998 and 2004, with an annual increase estimated at 6.31 %. The significant upward trends from both surveys strongly suggest that the population is increasing in Britain.

1.2 *Physiology and ecology*

R. hipposideros is one of Britain's smallest chiropterans (Stebbings and Griffith 1986). It is easily distinguishable due to the presence of a specialised nose-leaf used in echolocation and by its small size (body mass of between 4-9 g depending on season and reproductive status, and forearm length of 34-43 mm). The species is broad-winged, which coupled with its low body weight results in low wing-loading and low aspect ratio (Ransome 1990). It is therefore highly manoeuvrable, being able to turn in a small volume of space without reduction of speed, and shows low-speed agility, easily changing direction at low-speeds only (Norberg and Rayner 1987).

The reproductive cycle is similar to most temperate insectivorous bat species. Mating takes place in late autumn and semen is stored by the female over winter. Ovulation occurs in early spring and birth in mid-summer (Racey 1982). Females give birth to one young between early June and mid-July (Schober and Grimmberger 1993). In a study in south Poland, the reproductive success (ratio of

juveniles/adults) ranged from 0.21 to 0.29 (Kokurewicz 1997). Young are weaned within about six weeks. Juveniles reach full adult size in about 70 days but the majority do not becoming sexually mature until they are 1 year old (Gaisler 1966).

Early ringing studies demonstrated the sedentary nature of *R. hipposideros*, which rarely moves more than 5 km (Hesketh 1951, Hooper and Hooper 1956), although the species is known to migrate long distances, exceeding 146 km (Harmata 1989). Female *R. hipposideros* demonstrate great fidelity to their maternity roosts but move freely between nearby winter roosts. Summer roosts occur in buildings although historically, *R. hipposideros* is believed to have roosted all year round in caves (Gaisler 1963a). Maternity roosts occur predominantly in roof voids of 19th century buildings with stone walls and slate roofs (Schofield 1996), although a wide range of structures are utilised (e.g. church towers, farm outbuildings, former prison cells; pers. obs.). In winter *R. hipposideros* roosts in mines, caves, cellars and other underground structures. It selects sites with high humidity and temperatures between 4 and 12 ^{o}C (Ransome 1991).

1.3 *Threats*

A number of threats to the species have been identified, including changes in native species dynamics, such as the prey base (IUCN 2004). Loss of roosting sites, through deterioration, renovation and remedial timber treatment is also a continuing problem, together with disturbance to hibernation sites (Hutson 1993, Anon 1995, Hutson et al. 2001).

However habitat loss and fragmentation are probably the greatest threats to *R. hipposideros*. Nearly half of the variation in extinction risk in bat species can be explained by small geographical range sizes and species with low aspect ratios are especially at risk (Jones et al. 2003). Smaller geographic ranges may reduce the likelihood of a population surviving dramatic fluctuations in size. Low aspect ratio wings are associated with species that have smaller foraging ranges, are poorer dispersers, and are generally not migratory, limiting their ability to adapt to changing habitats.

The most important cause of habitat fragmentation is the expansion and intensification of land-use through intensive farming practices (Burgess and Sharpe 1981). 75 % (18.3 million hectares) of the land in Britain is used for agriculture (Robinson and Sutherland 2002) and its management is perhaps the single most important factor for mammal conservation in Britain (Macdonald and Johnson 2003). The degree of intensification varies across the country. For example arable farming now dominates in the east and pastoral farming in the west and the recent crisis in the beef industry has resulted in a spread of arable land further westwards. There was significantly less improved grassland in 1998 than 1990 in the western lowlands of England and Wales, and significantly more arable land (Haines-Young et al. 2000). Other documented effects of intensification include: loss of 23 % of hedges and 75 % of ponds between 1984 and 1990 (Entwistle et al. 2001) and an increase in average field sizes (Westmacott and Worthington 1997). Research has shown there has been a corresponding decline in the biodiversity in lowland farmland, for example, invertebrates (Benton et al. 2002), brown hare *Lepus europaeus* (Smith et al. 2004) and farmland birds (Donald et al. 2001).

A minority of agricultural land is farmed organically. Organic and in-conversion production accounts for just 4 % of UK farmland (Soil Association 2004). Organic farms are characterized by more complex crop rotations, more grass ley, and higher and wider hedges (Feber et al. 1997, Feber et al. 1998). Fuller *et al.* (2005) also found that the proportion of land that was grass rather than arable land was much higher on organic than non-organic farms and the density of hedges was higher. A number of comparative studies of organic and conventional systems have been undertaken that identify a range of taxa, including invertebrates, mammals and birds, that benefit from organic management (Wilson et al. 1997, Feber et al. 1998, Chamberlain et al. 1999). Of particular note is a study by Wickramasinghe *et al.* (2003) that demonstrated significantly higher bat activity on organic farms compared with conventional farms.

An extension of organic farming could therefore contribute to the restoration of biodiversity in agricultural landscapes (Fuller et al. 2005). However a review by

Hole *et al.* (2005) suggests that it remains unclear whether a 'holistic' approach (i.e. organic) provides greater benefits to biodiversity than carefully targeted management prescriptions applied to relatively small areas of cropped and/or non-cropped habitats within conventional agriculture (i.e. agri-environment schemes). Benton *et al.* (2003) also argue that future research should develop management solutions that recreate heterogeneity as the key to restoring and sustaining biodiversity in temperate agricultural systems. Agri-environment schemes have been used successfully in Britain to aid the long-term conservation of a range of species of conservation concern, for example Cirl bunting *Emberiza cirlus* (Peach et al. 2001), butterflies (Pywell et al. 2004), bumblebees (Pywell et al. 2006).

Racey (1998) states that foraging habitats must be protected if further declines in bat populations are to be halted and financial incentives are needed to stimulate management of farmlands near roosts. However in Britain such protection and enhancement is currently limited to the foraging habitat of *R. ferrumequinum* (Racey 2000). Agri-environment schemes for this species may have contributed to a 58 % increase in numbers recorded at maternity sites in Devon since 1995 (Longley 2003). Therefore it is important that such schemes are also developed for other bat species of conservation concern.

The most appropriate agri-environment scheme currently available in Wales is Tir Gofal. It is a whole farm scheme, available throughout Wales to farmers and landowners (Countryside Council for Wales 1999). The principal element is mandatory land management of key habitats (including woodlands, hedgerows, traditional buildings, streams and rivers and individual trees) and optional restoration or creation of certain habitats or features (such as new woods and traditional field boundaries). Applications are selected on a farm-by-farm basis according to the degree of environmental benefit they offer. The scheme can be linked to the Organic Aid Scheme and Better Woodland for Wales (BWW) scheme.

BWW is a grant scheme for creating and improving woodlands (Forestry Commission Wales 2006). Crucially, the management plan must address the

protection of rare species and important habitats. The biodiversity value of the woodland, especially any semi-natural woodland, must be maintained and enhanced. Similarly, the Woodland Grant Scheme is run by the Forestry Commission in England and offers a number of grants such as the Woodland Improvement, Woodland Management and Woodland Creation grant schemes.

Within England, Environmental Stewardship is the most appropriate agri-environment mechanism. It is also a whole farm scheme and has three elements: Entry Level Stewardship (ELS), Organic Entry Level Stewardship (OELS), and Higher Level Stewardship (HLS) (Anon 2005a, 2005b). The Entry Level schemes involve a commitment to a choice of management options (e.g. management of hedgerows and woodland edges, provision of buffer strips). Management prescriptions aim to secure widespread environmental benefits but are not specific enough for targeted measures for many key species. In contrast the HLS aims to deliver significant environmental benefits in high priority situations. It involves more complex management, tailored to local circumstances.

1.4 *Protection*

R. hipposideros is protected under Schedule 2 of the Conservation (Natural Habitats, etc.) Regulations 1994 (Regulation 38) and Schedule 5 of the Wildlife and Countryside Act 1981. It is listed in Appendix II in the 'Bonn' Convention on the Conservation of Migratory Species of Wild Animals 1979, for which conservation and management agreements are required by all member states. It is a Priority Species under the UK Biodiversity Action Plan (Anon 1995) and is also included in numerous county and local authority Biodiversity Action Plans within its range. The species is also covered by the Agreement on the Conservation of Populations of European Bats (UNEP/EUROBATS) (1991), which states the need to identify and protect important feeding areas for *R. hipposideros*.

Under the EC Habitats and Species directive 1992, seven sites within Britain have been selected as Special Areas of Conservation (SAC) designation for *R. hipposideros*. The sites include large populations of *R. hipposideros* and cover the

geographical range of the species. Sites have been selected, where possible, as composites of maternity and hibernation sites considered to belong to a single population or group of closely-associated populations. A further six SACs occur where the presence of *R. hipposideros* is a qualifying feature, but not a primary reason for site selection. While the series of SAC sites makes a contribution to securing favourable conservation status for *R. hipposideros* in Britain, wider measures such as specified under the UK Biodiversity Action Plan are also necessary to support its conservation in Britain.

1.5 *Wider context*

Chiroptera make a huge contribution to global mammalian biodiversity with over 1100 species worldwide (Simmons 2005) and their diversity is reflected in highly varied roosting and feeding behaviours, and social organization (Altringham 1996). Bats make valuable indicators of the integrity of the environment, due to their small size, mobility and longevity (Fenton 1997). Insectivorous bats in particular are good 'bioindicators' because of their dependence on a range of habitats, reliance on insect prey and sensitivity to prevailing climatic conditions. However as Fenton (2003) highlights, lack of information about habitat use by specific species means the full potential of using bats as indicator species for a particular habitat or ecosystem may be unrecognised.

R. hipposideros have potential to also become an indicator species, particularly given their distinctive appearance and echolocation. However in common with other bats whilst they capture the public imagination they can also have a pubic image problem (Fenton 2003), particularly as their roosts are typically in buildings, which can lead to conflict.

1.6 *Previous studies*

As has been highlighted, to understand the full potential of using *R. hipposideros* as a flagship species requires more detailed information about their habitat and landscape use. To date the species has been relatively understudied, despite being described as one of the most endangered European bat species (Stebbings 1988). This is in contrast to *R. ferrumequinum* which has been subject to extensive research over the years, including one of the longest running mammal studies in the world, undertaken in Britain since the 1950s (Ransome 1990).

The relative lack of research into *R. hipposideros* is in part due to the species' highly directional echolocation calls that make it difficult to record them in the field using ultrasound bat detectors. However investigations have been undertaken on some aspects of the species' biology, including echolocation (Jones and Rayner 1989, Jones et al. 1992), habitat use (McAney and Fairley 1988b, Schofield 1996), postnatal growth and reproductive biology (Gaisler 1966, Reiter 2004b) and diet (McAney and Fairley 1989, Williams 2001).

Over the last two decades more advanced study methods, such as radio-telemetry has been used to study the ecology of many birds and mammals (see reviews by Harris *et al.* (1990) and Godfrey and Bryant (2003)), including species of Chiroptera (see reviews by Fenton (1997, 2003)). Until lately the large size of transmitters prevented their use on low-mass Microchiroptera, such as *R. hipposideros* because the transmitters would exceed the recommended limits of justifiable increased weight of 5% at body masses <70g (Aldridge and Brigham 1988). Recent advances in radio-tag technology have led to the progressive miniaturisation of transmitters and several small-scale radio-tracking studies have now been undertaken on *R. hipposideros* (Bontadina et al. 2002, Holzhaider et al. 2002, Motte and Libois 2002).

One of the key advantages of radio-telemetry is the ability to obtain more accurate habitat use data from animals that are well dispersed or elusive and difficult to study (Kenward 2001a). However a fundamental assumption of wildlife studies

reliant on this method is that radio-tagged individuals are behaving in a similar manner to untagged animals (White and Garrott 1990) and yet the use of radio-transmitters on bats has consequences for both their energetic costs and their manoeuvrability (Fenton 2003).

Hickey (1992) studied the effect of transmitters on the foraging success of *Lasiurus cinereus* bats using tags representing on average 3.1 % of the body mass and found no significant difference between foraging success with or without transmitters. However Aldridge and Brigham (1988) measured the flight maneuverability of loaded and unloaded female *Myotis yumanensis* bats and their results suggested that increases in body mass of 5 to 33% resulted in reduced maneuverability. They suggested that a small decrease in maneuverability could significantly decrease foraging efficiency. Rayner *et al.* (1989) state that all mass changes should be reflected in flight performance, which in turn influence behaviour and foraging strategy. The authors conducted experiments on an *Eptesicus serotinus* bat carrying a radio-transmitter 6.7% of its mass and showed how the bat adjusted wingbeat kinematics to maintain optimal muscle performance. The main consequence of loading was a marked rise in mechanical power, although the speed of the bat when loaded was not significantly different from unloaded. They suggested that other bats should adopt similar patterns when loaded, although experiments were undertaken in captivity and their results may not fully reflect conditions in the wild.

Several reviews have highlighted the fact that the majority of radio-telemetry studies fail to refer to the potential effects of tagging on the study animals. For example, in an analysis of 1990s radio-tracking literature Godfrey and Bryant (2003) reported only 10.4 % of 836 studies directly addressed the effect of radio-tags on their bearers. Similar concerns have been raised by Fenton (2003) in a review of radio-tracking studies of bats. Documenting the effects of radio-transmitters ideally requires a comparison between tagged and untagged controls (Withey et al. 2001). Irvine *et al.* (2007) assessed the impact of two types of radio transmitters on flight performance in racing pigeons and found that birds fitted with sacral-mounted radios flew more slowly and lost more weight and condition

than control birds whereas birds fitted with tail-mounted radios performed similarly to the control group.

However it is not possible to do a similar comparison between tagged and untagged controls with species such as *R. hipposideros* as it is not possible to gain comparable habitat use and behavioural data using non-invasive techniques such as ultrasound bat detectors. As a minimum therefore it is necessary to undertake a simple direct evaluation of behavioural or physical changes (e.g. skin abrasions, changes in body mass) (Withey et al. 2001) whilst Fenton (2003) recommends fully disclosing the sizes of tagged bats and transmitters used, together with the dates of tagging.

Two of the three previously published academic radio-tracking studies on *R. hipposideros*, radio-tracked only one individual, partly due to concerns with the high sensitivity of the species to disturbance. Holzhaider *et al.* (2002) tracked a lactating female (weight 5.4 g) using a 0.4 g tag whereas Motte and Libois (2002) used a transmitter weighing 0.65 g on an adult female during post-lactation in August (weight of bat not stated but tag indicated to be 10 % of the bat weight). Both authors report reduced activity on the first night on release after the tagging procedure (3 hours and 16 mins respectively).

The more extensive study by Bontadina *et al.* (2002) used transmitters ranging in mass from 0.332 to 0.440 g that increased the body mass of tagged individuals by 4.5-8.1 %. One of the tagged bats returned to the roost on release after tagging whilst the remaining animals (n = 11) spent a period of 20-150 min either roosting or perched in trees close to the release point before foraging. The authors discuss in detail the potential effects of tag bearing on *R. hipposideros* and conclude that the tracking sessions should not have artificially altered the bats foraging behaviour. However their findings suggest that only the lowest mass tags should be utilised, heavily pregnant females should be avoided and data from the first night should be omitted from analyses as the bats seem to display atypical behaviour following the tagging procedure.

1.7 *Review of other radio-telemetry studies*

The species has been subject to a number of radio-tracking studies in Britain undertaken by professional ecologists commissioned by governmental bodies, charities or private clients, often in response to development pressures such as new road build. An attempt has been made to collate this work as reports are not always in the public domain. Such studies represent a valuable opportunity to assess ranging behaviour and habitat use on a local and possibly regional scale, allowing a detailed picture of patterns of landscape use to be built up across the range of *R. hipposideros* in Britain. Details are provided below and the key range parameters, where revealed, are summarised in Table 1.1. For a description of range attributes please refer to Section 3.3.3. Data from the published academic radio-tracking studies detailed above have also been included.

Source	Location	Sex	Status	*n*	100% MCP/ha		Max distance/km		Range span/km	
					Mean	Range	Mean	Range	Mean	Range
Stebbings (2000)	Gwynedd, Wales	M	AD	1			*c.* 1.7			
		F	NP	1			*c.* 1.5			
Billington (2001)	Gwynedd, Wales	M	AD	3			Max *c.* 9			
		F	PL	4						
		F	JUV	1						
Billington (2002)	Gwynedd, Wales	F	P?	5						
Bontadina *et al.* (2002)	Monmouth-shire, Wales	F	PL	5	18.0[a]	1.0-57.9[a]	0.5[a]	0.3-0.9[a]		
		F	NP	3	207.9[a]	25.7-368.4[a]	2.6[a]	1.0-4.2[a]		
Cresswell Associates (2002)	Gloucester-shire, England	M	AD	9	254	34-625			2.4	1.0-4.4
		F	PL	5	386	71-1155			2.9	1.5-4.9
		F	JUV	1	447	-			4.1	-
Holzhaider *et al.* (2002)	Bavaria	F	L	1	-	-	3.6	-		
Motte and Libois (2002)	Belgium	F	PL	1			1.2[b]	-		

Table 1.1. Key range parameters where revealed during previous radio-tracking studies on *Rhinolophus hipposideros* in Europe.

Source	Location	Sex	Status	*n*	100% MCP/ha		Max distance/km		Range span/km	
					Mean	Range	Mean	Range	Mean	Range
Schofield *et al.* (2002)	Radnor, Wales	F	P	6	92.7	28.6-151.8	1.7			
		F	L	1	11.8	-	0.5			
		F	PL	4	124.0	31.6-353.0	1.4			
Billington (2003)	Gwynedd, Wales	M/F	T	3						
Andrew McCarthy (2003)	Devon, England	M/F	AD/ NP	10						
Smith and Morgan (2003)	Powys, Wales	F	T	6						
			T	1			3.0			
Billington (2006)	Minffordd, Wales	F	P?	10						
			L/NL	6						
			NP	3						
			JUV	3						
		M	JUV	1						
Smith Ecology Ltd (2006)	Usk, Wales	M	AD	16			6.7+			
		F	L	2						
			NP	1						

Table 1.1. (cont.)

Table 1.1. Key range parameters where revealed during previous radio-tracking studies on *Rhinolophus hipposideros* in Europe. 100% MCPs (minimum convex polygons) (Mohr, 1947) are home ranges. Maximum distance is the furthest tracked location away from the roost and range span is the maximum width of the 100% MCPs. Key to abbreviations in table:

Sex: M, male; F, female

Status: AD, adult; NP, nulliparous; JUV, juvenile; P, pregnant; L, lactating; NL, not lactating; PL, post-lactation; T, transitional between hibernation and summer roosts

[a] authors state that the home range of 3 adult and 1 immature individuals tracked had not reached asymptotes so should be regarded as minimum values.

[b] authors state maximum range of the animal was presumably greater than 1.2 km.

The majority of studies have been undertaken at and around a large maternity colony (believed to be one of the largest colonies in Europe) in Gwynedd, Wales. The studies have been commissioned by Countryside Council for Wales (CCW) to assess impacts on the colony by the A487 and A499 road improvement schemes. Two *R. hipposideros* (1 male, 1 immature female) were radio-tracked in June 2000 (Stebbings 2000). Details of ranging behaviour are not provided but from a figure of recorded foraging areas I have inferred the bats appear to be recorded maximum *c.* 1.7 km and *c.* 1.5k m respectively from the maternity roost. The author states the importance of woodland since 'almost all the time spent by the two bats while dispersing or foraging was in or very close to tree cover'. Eight *R. hipposideros* were radio-tracked from the roost and a nearby hibernation site in September 2001 (3 male, 4 adult female, 1 juvenile female) (Billington 2001). Details of ranging behaviour and habitat use are limited but the bats were recorded in 36 1-km squares (based on British national grid) and a male bat was recorded up to 9 km away from the roost. A further five adult female *R. hipposideros* were radio-tracked from the colony in May 2002 (Billington 2002). Again details of ranging behaviour are limited but bats were recorded foraging in 10 1-km squares (based on British national grid). Billington (2003) radio-tracked three *R. hipposideros* (1 male, 2 female) from a nearby hibernation site in April 2003. From a figure of recorded foraging areas I have inferred the bats appear to be recorded maximum *c.* 1.1 km from the hibernation site.

Ten *R. hipposideros* (1 male, 7 adult female, 2 immature female) were radio-tracked from night roosts associated with two maternity colonies in Devon,

England, during May, August and September 2003 (AndrewMcCarthyAssociates 2004). The study was commissioned in response to a proposed road improvement scheme. The work demonstrates the colonies use separate feeding zones with no range overlap but it was not possible to infer ranging behaviour or habitat use from the information supplied. Smith and Morgan (2003) radio-tracked six female *R. hipposideros* in Powys, Wales, in April 2003. The study aimed to locate summer roosts, foraging areas and commuting routes associated with a large hibernation site (max count 300+). They identified day roosts that ranged between 5.7 km and 24.1 km from the hibernation site and a foraging area within damp alder *Alnus glutinosa* / birch *Betula* spp. woodland 3 km distant from one of the day roosts.

The above studies were limited by time and budget constraints and are all characterised by small sample sizes. In contrast a more comprehensive radio-tracking study was undertaken in Gloucestershire, England, by Cresswell Associates (2004) on behalf of The National Trust. Fifteen *R. hipposideros* (9 male, 5 adult female, 1 juvenile female) were radio-tracked successfully during June to September 2003, with only males tracked in the pre-natal and lactation periods (June and July) and predominately females in the post-lactation period (August and September).

The mean nightly distance travelled by males was 21.29 km (n = 8; range 1.30-13.35 km), by adult females was 7.36 km (n = 5; range 3.88-11.79 km) and by a juvenile female was 15.83 km (n = 1). The authors report that bats were found to spend typically 20-25 % of their night's activity in night roosts, rising to more than 30 % (and in one case almost 50 %) at the end of September. They also considered habitat preferences and found that woodland and scrub/garden habitats were the most consistently selected habitats overall and there was a significant preference for grazed over ungrazed grasslands. The avoidance of arable land was highlighted.

1.8 *Aims*

The study intends to satisfy section 5.5.2 of the UK Biodiversity Action Plan for *R. hipposideros* that states a need to 'undertake research to identify the habitat requirements of this species and the appropriate management of feeding areas needed to maintain populations at a favourable conservation status' (Anon 1995). The Action Plan further states that 'the findings should be used to inform development of guidelines and policies for habitat protection, creation and management around roost sites'.

The key objectives of this study are fivefold. First, to investigate foraging and night roosting behaviour by *R. hipposideros,* and to quantify foraging and home ranges. Second, to quantify habitat use by the species. Third, to determine the summer diet of *R. hipposideros* and investigate whether their diet reflects possible seasonal changes in habitat use. Fourth, to assess whether surrounding landscape influences foraging and ranging behaviour, habitat use and selection, and diet. To meet these objectives and allow geographical variations to also be investigated bats have been studied within three maternity roosts representing the key landscape types that characterise the distribution of *R. hipposideros* in Britain: i) lowland farmland under pressure from agriculture and development; ii) high quality landscape supporting exceptional populations of *R. hipposideros*; and iii) upland fringe. The first two key landscape types (lowland farmland and high quality) fall under the type 'westerly lowlands' (England/Wales) within the seven 'Environmental Zones' described by the UK Countryside Survey, whereas the third type corresponds to the 'uplands' (England/Wales) zone (Haines-Young et al. 2000). Finally, the study aims to make an assessment of whether the habitat use and foraging behaviour of juvenile bats is similar to the adult females within a lowland landscape.

1.9 *Thesis organisation*

In Chapter 2, the diet of *R. hipposideros* is reviewed and a dietary study, undertaken to assess the summer diet of the species across three different landscape zones in Britain, is outlined. I evaluate whether the results provide evidence for the existence of seasonal and geographical variation in the diet.

In Chapter 3, a radio-tracking study to assess the foraging behaviour of *R. hipposideros* across three different landscape zones in Britain is described. I evaluate the seasonal variations in behaviour and determine how landscape quality and fragmentation may influence colony size.

In Chapter 4, I describe the night roosting behaviour of *R. hipposideros* during the radio-tracking study and evaluate differences in behaviour through the breeding season and highlight the importance of night roosts in conservation planning.

In Chapter 5, I evaluate whether *R. hipposideros* are using habitats according to availability, and determine which habitats are utilised. A comparison between habitat use in three different landscape zones through the breeding season is undertaken. Where possible, the results are compared to those obtained from other radio-tracking studies, and their implications for conservation management are considered.

All of the above chapters are structured as papers, and therefore each comprises a Summary, Introduction, Methods, Results and Discussion. Chapter 6 is a general discussion, in which all the results are summarised and related to each other, and conclusions are made, particularly in reference to the conservation of *R. hipposideros* in Britain.

CHAPTER TWO

SUMMER DIET OF *R. HIPPOSIDEROS*

2 Summer diet of *R. hipposideros*

2.1 *Summary*

I examined the diet of *R. hipposideros* during the breeding season using faecal analysis of samples from sites in four counties of England and Wales. The localities represented three different landscape types: lowland, upland, and a landscape considered to be of high quality for the species. In total, I analysed 1112 faecal pellets collected in 71 samples over a period of three years (2003-5).

The diet included 33 individual prey categories (identified principally to family level) comprising 11 orders of arthropods: Diptera (between 32 and 41 % frequency of the diet across sites), Lepidoptera (15-26 %), Neuroptera (9-15 %), Trichoptera (5-20 %), Hymenoptera (9-15 %), together with Psocoptera and Coleoptera, and traces of Ephemeroptera, Hemiptera, Aráneida, and Opiliones.

Although the diet of *R. hipposideros* was fairly consistent between sites in terms of major prey categories consumed - Tipulidae, Anisopodidae, Scatophagidae, Lepidoptera, Hemerobiidae, Trichoptera and Ichneumonidae, and there was no difference in dietary breadth at the paired sites, the composition of the diets did differ significantly geographically. Variations were particularly noticeable prior to the birth of young. Differences between the lowland and high quality landscapes, and the lowland and upland landscapes were in particular highly significant. There was also significant seasonal variation in diet at each locality and interannual variation at the lowland site.

Although the presence of non-volant prey in the diet confirms gleaning, I suggest that given their specialised echolocation, gleaning is unlikely to be the principal foraging strategy with the majority of prey caught on the wing during aerial hawking. Feeding on swarming insects at dusk and dawn could play an important part in foraging.

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2.2 *Introduction*

R. hipposideros has undergone a dramatic decline in western Europe and is regarded as endangered in many regions (Stebbings 1988, Ohlendorf 1997). The British and Irish populations are considered to be internationally important and now form one of the European strongholds (Macdonald and Tattersall 2001), despite being at the northern limit of the European distribution. In contrast to the situation across much of Europe, the British population is believed to be increasing (Bat Conservation Trust 2004) and is estimated at 18,000 individuals (Battersby 2005) with at least 10,000 of these occurring in Wales (Altringham 2003). Within Britain, populations of *R. hipposideros* occur both within the lowland farmland landscape and within areas of upland, characterised by open moorland.

Dietary investigations are a vital component of autoecological studies of bats and Kunz and Whitaker (1983) have shown that the analysis of faeces is a valid method to determine the diet of insectivorous bats. Although there have been eight systematic studies of the summer diet of *R. hipposideros* in Europe using faecal analysis (Poulton 1929, Leishman 1983, Beck et al. 1989, McAney and Fairley 1989, Hollyfield 1993, Beck 1994-1995, Arlettaz et al. 2000, Williams 2001) none has yet covered the Welsh or upland populations. Although only a limited number of studies have considered spatial variation in diet of insectivorous bats (Anthony and Kunz 1977, McAney and Fairley 1989, Sample and Whitmore 1993, Whitaker 1995, Johnston and Fenton 2001, Zhang et al. 2005) they have all shown differences do oocur. For example, McAney and Fairley (1989) demonstrated variation in diet composition of *R. hipposideros* among localities in Ireland. Nine food categories showed significant variation between roosts, despite similar surrounding terrain, predominantly permanent pasture with mixed hedgerows and occasional small mixed woodland strips, although local differences in open/running water and woodland cover did occur. Therefore I hypothesise that the diet composition of *R. hipposideros* will vary among localities in Britain. Furthermore I expect diffences to be more pronounced among lowland and upland landscapes where greater differences in surrounding habitat composition occur. This could have implications for the conservation of the species in Britain and

management plans may need to take account of local or regional differences in diet.

I examined the diet of *R. hipposideros* within three distinct landscape types in Britain to determine whether spatial and seasonal variation exists.
The specific aims of this chapter are:

1. To investigate whether the diet within a colony remains relatively unchanged from year to year.
2. To test the hypothesis that the diet varies between different landscape types in Britain.
3. To investigate any seasonal changes in diet composition.
4. To describe any similarities between my study and previous work on the diet of *R. hipposideros*.

2.3 *Methods*

2.3.1 *Study sites*

I conducted the study of *R. hipposideros* during the summers of 2003, 2004 and 2005 within four maternity roosts representing the key landscape types that characterise the distribution of *R. hipposideros* in Britain.

North Somerset and Wiltshire occur within the centre of the range of *R. hipposideros* in Britain and were selected to provide a representative example of the lowland landscape type, being under pressure from both intensive agriculture and development. Roost A was a maternity colony of *c.* 160 animals (including juveniles) located in the attic space of a converted barn in the village of Upper Langford, North Somerset (51°19'N, 2°46'W, *c.* 40 m above sea level). The landscape to the north, west and south-west is lowland farmland, the majority being pasture, with some arable. To the south-east lies the open heathland of the Mendip Hills, which features an extensive wooded scarp at its northern edge.

The Wye Valley and Forest of Dean region (Monmouthshire and Gloucestershire) supports an exceptional population of *R. hipposideros*, with the greatest

concentrations of the species found in Britain, totalling about 26% of the national population. There is a high density of sizeable maternity roosts, some of which are among the largest in Europe. The complex of sites has been designated a Special Area of Conservation (SAC) (Wye Valley and Forest of Dean Bat Sites, SAC EU code UK0014794). Special Areas of Conservation are strictly protected sites designated under the EC Habitats Directive. The site covers 142.7 ha, of which 26.2% comprises broad-leaved deciduous woodland (http://www.jncc.gov.uk/protectedsites/sacselection/sac.asp?EUcode=UK0014794). The level of woodland cover is considerably higher than the national average. In England broad-leaved woodland comprises 5.8% of the total surface area and in Wales it comprises 6.1% (figures calculated from data as of 31 March 2007 supplied by the Forestry Commission http://www.forestry.gov.uk/forestry\AHEN-5G5GN7). Broad-leaved deciduous woodland is a key foraging habitat for *R. hipposideros* (Bontadina et al. 2002). Therefore given the extent of woodland cover I have classified the Wye Valley and Forest of Dean landscape as high quality for the species. Roost B was a maternity colony of *c.* 750 bats within a small barn in the village of Brockweir, Gloucestershire (51°43'N, 2°40'W, *c.* 120 m above sea level). The landscape is dominated by the River Wye, which features broad-leaved woodland on the valley slopes. Sizeable areas of forestry plantation also exist. Elsewhere the landscape is agricultural and predominantly comprises pastoral habitats. Within the vicinity of the roost exists an area of former wood pasture that now comprises a network of very small flower-rich fields and unmanaged hedgerows and tree belts.

Roost C was a maternity colony of *c.* 130 animals within a large barn in the village of Llanbedr, in the Brecon Beacons National Park (51°53'N, 3°06'W, *c.* 247 m above sea level). The roost occurs in a valley characterised by numerous small streams, pasture farmland and sizeable areas of forestry plantation. Above the valley the landscape is dominated by open heathland/moorland.

Roost D was a maternity colony of *c.* 160 animals located in the attic space of a 19th century house in the village of Limpley Stoke, Wiltshire (51°21'N, 2°19'W, *c.* 75 m above sea level). The lowland landscape is dominated by the River Avon and Kennet and Avon Canal to the east and Midford and Wellow Brooks to the

west. Extensive woodland occurs on the valley slopes with remaining areas predominantly pastoral land.

For details of proportions of habitats surrounding roosts A-C refer to Figure 5.1, Chapter 5.

2.3.2 *Collection and analysis of droppings*

At all sites I collected faeces in plastic seed trays lined with paper positioned below the main roosting place. Twelve samples were collected at fortnightly intervals from April to September from Lowland A and Lowland D in 2003, High Quality B in 2004 and Upland C in 2005. Trays were re-set on collection dates. To allow comparison between data and the assessment of the diet within a lowland landscape more fully, Lowland A was studied in each of 2003, 2004 and 2005 survey sessions. The years and dates on which material was collected from each roost are given in Table 2.1. Trays were re-set on collection dates.

	Collection date		
Sample	2003 Roost A+D	2004 Roost A+B	2005 Roost A+C
Trays set	2 April	5 April	5 April
1	16 April	19 April	19 April
2	30 April	3 May	3 May
3	14 May	17 May	17 May
4	28 May	31 May	31 May
5	11 June	14 June	14 June
6	25 June	28 June	28 June
7	9 July	12 July	12 July
8	23 July	26 July	26 July
9	6 August	9 August	9 August
10	20 August	23 August	23 August
11	3 September	6 September	6 September
12	17 September	20 September	20 September

Table 2.1. The years and dates on which samples of faecal material were collected from each *Rhinolophus hipposideros* roost. The start date on which sample 1 commenced is also given. There is no sample 1 for Lowland D roost.

Each tray was examined for discarded insect fragments which were removed and the batch of droppings was air dried for several days before storage. A sample of 16 droppings was selected at random from each sample. The entire sample was shaken onto a graph drawn on graph paper and a random number table used to determine *x* and *y* co-ordinates. The nearest intact dropping (some droppings had broken into segments) was removed for analysis. Sixteen droppings were analysed following Whitaker (1988) and to give a comparison with previous dietary studies of *R. hipposideros* undertaken in Ireland in which 30 droppings per month were analysed (McAney and Fairley 1989) and in England in which fortnightly samples of 20 droppings were analysed (Williams 2001). To check that an adequate number of droppings had been analysed per sample, plots of the number of different prey categories *vs.* number of droppings were done to confirm asymptotes had been reached. Two samples from Lowland D had fewer than 16 droppings, in which case all intact faeces were examined ($n = 4$ for sample 5 and 12), and sample 1 was absent due to lack of access.

Individual pellets were softened in hot water for at least one hour and teased apart in glycerine to aid separation under a dissection microscope. Recognisable arthropod fragments were mounted on slides and identified using various publications (Coe et al. 1950, Tilling 1987, Whitaker 1988, Unwin 1991, Chinery 1993, Shiel et al. 1997), and a reference collection of arthropods captured in the vicinity of roosts A, B, and C during the radio-tracking work using a sweep net. A reference collection compiled by Williams (2001) was also used. Prey was usually identified to order or sub-order, but family level was possible for Neuroptera, Diptera and Coleoptera. Lepidopteran scales may persist in the digestive tract for long periods (Whitaker 1988, Robinson and Stebbings 1993), so only pellets that contained very abundant scales (typically covering the Petri dish) or other fragments characteristic of moths were used to score the presence of this order. Where it was not possible to identify a particular fragment, this was scored as an 'unidentified' prey category.

2.3.3 *Data analysis*

The results were expressed in two ways to allow comparison with other studies: *percentage occurrence* (the number of pellets *n* in which a category *c* is present, n_c, divided by the total number of pellets examined and multiplied by 100) and *percentage frequency* (n_c divided by $\sum n_c$ for all categories multiplied by 100). Other studies have quantified the diet by estimating the percentage volume of a prey type (sum of estimated % volume in individual pellets, divided by total volume of sample, multiplied by 100) (Jones 1990, Agosta et al. 2003). However I was unable to reliably use this method due to the small size of the prey items consumed, and the lack of diagnostic features on many of the arthropod fragments.

Statistical analyses to assess variation in each prey category over the summers (between samples) and between roosts consisted of randomized contingency tables (χ^2) using the numbers of occurrences. To satisfy the mathematical assumptions underlying the chi-square distribution, it was necessary to combine some seldom occurring prey categories to ensure i) that no expected value was less than 1; ii) and no more than 20 % of expected values were less than 5 (Ashcroft and Pereira 2003). To avoid the potential accumulation of decision (Type I) errors resulting from multiple testing, the Bonferroni procedure was used to adjust the critical value to $\alpha = 0.05/5 = 0.01$ (Quinn and Keough 2002).

Following Jones (1990), the Shannon-Wiener index of diversity (H') was calculated as a measure of diet breadth (Krebs 1999) and to estimate the degree of specialization in the diet. Indices were calculated using 33 prey categories. Two-way ANOVA (without replication) was used to assess variation in indices between roosts and between samples.

2.4 *Results*

In total, I analysed 1112 faecal pellets collected in 71 samples from four roosts. Analysis of variance showed that among years the samples were collected on similar dates (using Julian days) (ANOVA, $F_{2,36} = 0.002$, NS).

33 individual prey categories were identified comprising 11 orders of arthropods. In addition mites (order Acari), ticks (Argasidae) and flea eggs (order Siphonaptera) were recorded. These have not been included in the analyses as it is likely that these were either ingested during grooming or collected with the droppings. Tipulidae and Trichoceridae were treated as a combined category, as were Chironomidae and Ceratopogonidae, and Calliphoridae and Muscidae, as it was not possible to distinguish reliably between these families. Three families of Trichoptera were identified: Polycentropidae, Hydropsychidae and Limnephilidae, with the latter family being the most abundant. However, not all fragments were identifiable to family level so all were recorded as Trichoptera.

Geographical variation – pooled data

The major prey orders were Diptera (32-41 % of the diet according to site), Lepidoptera (15-26 % of the diet), Neuroptera (9-15 % of the diet), Trichoptera (5-20 % of the diet) and Hymenoptera (9-15 % of the diet), together with Psocoptera and Coleoptera, and traces of Ephemeroptera, Hemiptera, Araneida, and Opiliones. Of the Diptera the sub-order Nematocera was the most abundant (64-78 % of Diptera), followed by Cyclorrhapha (19-33 % of Diptera) and Brachycera (2-8 % of Diptera).

The data are represented as percentage occurrence in Figure 2.1. Randomized contingency tables yielded significant differences in overall diet composition between each pair of localities, with highly significant differences between lowland and high quality, and lowland and upland sites.

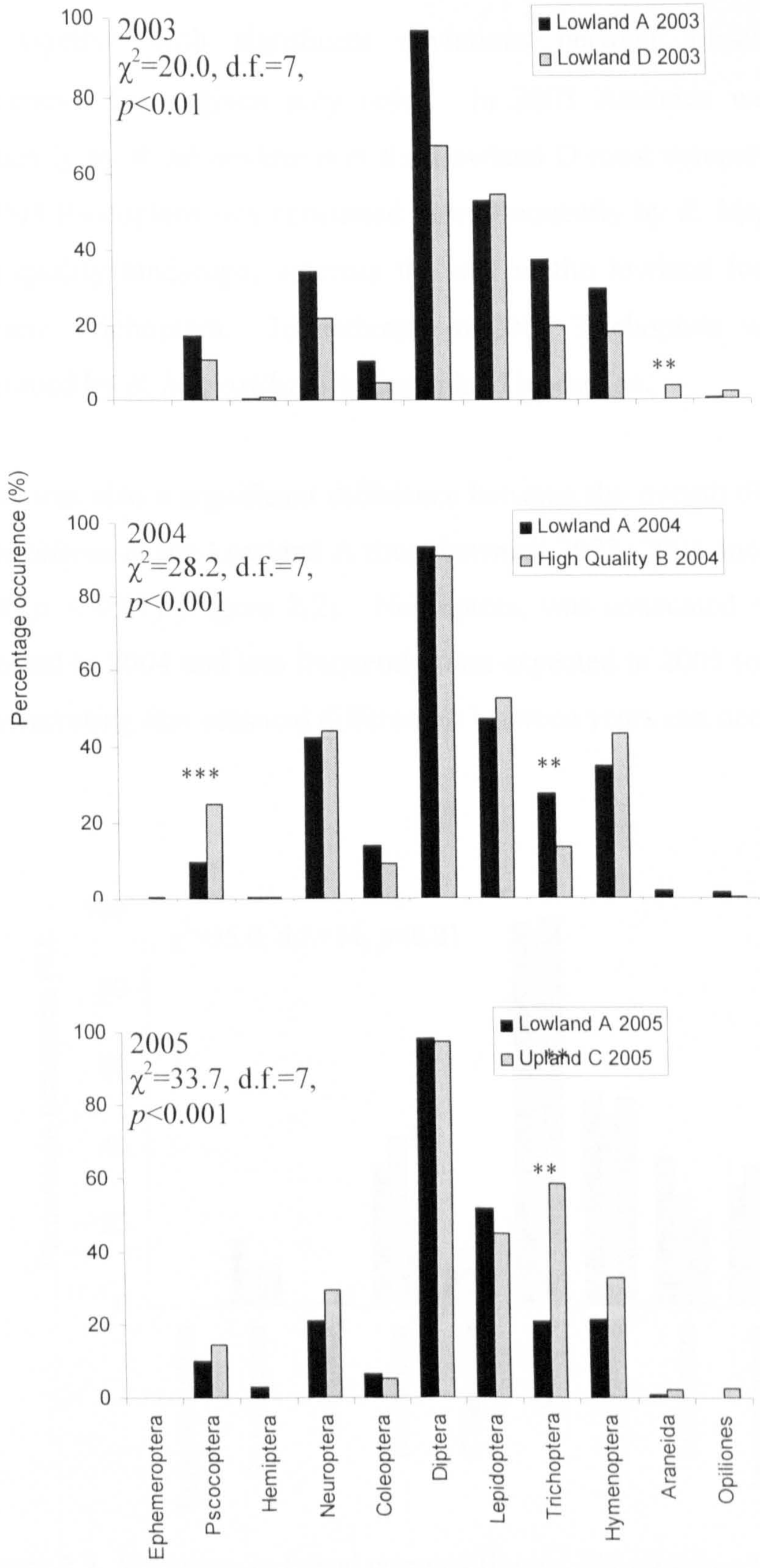

Figure 2.1. Geographical variation in faecal composition of *Rhinolophus hipposideros* (based on prey orders) within four localities across 2003-5. Overall results of the randomized contingency tables are indicated in the frame, whereas significant deviations between observed and expected frequencies for a given prey order are represented by ***=p<0.001, **=p<0.01.

The randomized contingency tables for the overall results are indicated in Figure 2.1, together with significant deviations between observed and expected frequencies for a given prey order. In 2003 Araneida were consumed more frequently by *R. hipposideros* at the Lowland D roost compared with Lowland A. In 2004 Psocoptera was consumed more frequently by *R. hipposideros* within the high quality landscape, whereas the diet at the lowland locality featured more frequent Trichoptera. In contrast, in 2005 Trichoptera was more frequently consumed by *R. hipposideros* in the upland landscape.

There was also a significant difference between the overall diet composition of *R. hipposideros* at the Lowland A roost between 2003, 2004 and 2005 ($\chi^2 = 35.0$, d.f. = 14, $p < 0.01$) (Figure 2.2). Neuroptera, was consumed more frequently than expected in 2004 and less frequently than expected in 2005 (only at $p < 0.05$ level) demonstrating that seasonal differences between years can occur in a locality.

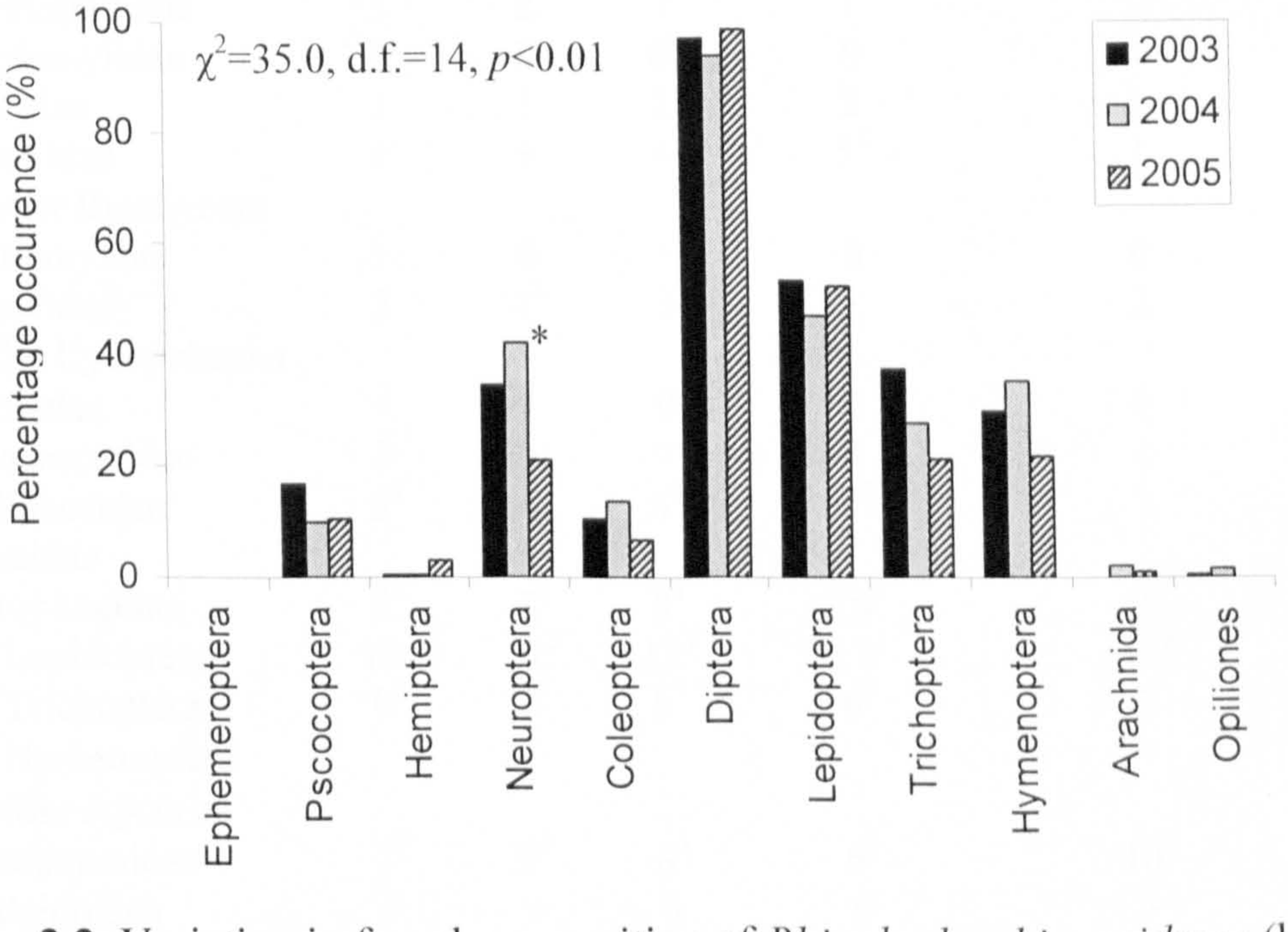

Figure 2.2. Variation in faecal composition of *Rhinolophus hipposideros* (based on prey orders) between 2003-5 at the Lowland A locality. Overall results of the randomized contingency table is indicated in the frame, whereas deviations between observed and expected frequencies for a given prey order are represented by *=p<0.05. Neuroptera was consumed more frequently than expected in 2004 and less frequently than expected in 2005.

	England			England/Wales	Wales
	Lowland A		Lowland D	High Quality B	Upland C
Prey category	2003	2004	2005	2003	2004	2005
Order Ephemeroptera	0	0	0	0	+	0
Order Psocoptera	4	3	3	4	6[7]	3
Order Hemiptera	+	0	1	+	+	0
Suborder Homoptera						
Aphidoidea	0	+	+	0	0	0
Order Neuroptera						
Hemerobiidae	8[5]	11[4]	5[8]	7[6]	10[4]	7[6]
Chrysopidae	+	1	1	+	+	0
Order Coleoptera	1	+	1	+	+	1
Suborder Adephaga						
Carabidae	0	0	1	0	0	+
Suborder Polyphaga						
Staphylinidae	0	+	+	+	0	+
Scarabaeoidea	2	3	+	1	2	1
Chrysomeloidea	0	+	0	0	0	+
Order Diptera						
Suborder Nematocera						
Tipulidae	15[1]	12[3]	20[1]	14[2]	13[1]	18[1]
Anisopodidae	15[2]	15[1]	17[2]	10[3]	13[2]	14[2]
Psychodidae	2	2	2	1	1	1
Culicidae	1	1	+	+	+	+
Chironomidae/						
Ceratopogonidae	+	+	+	2	1	1
Dixidae	1	+	+	1	+	+
Mycetophilidae	3	2	3	1	5[8]	6[8]
Cecidomyiidae	0	0	0	0	+	0
Sciaridae	1	1	2	2	2	3
Simuliidae	+	+	+	5[8]	1	2
Suborder Brachycera						
Stratiomyidae	+	0	+	0	0	0
Empididae	3	4[8]	3	1	2	2
Suborder Cyclorrhapha						
Syrphidae	+	1	0	0	+	+
Sphaeroceridae	3	3	2	1	4	1
Calliphoridae/	5[8]	4	6[5]	7[5]	3	4
Muscidae						
Scatophagidae	8[5]	7[6]	8[4]	10[4]	9[6]	6[7]
Order Lepidoptera	13[3]	12[2]	13[3]	17[1]	13[3]	10[4]
Order Trichoptera	9[4]	7[7]	5[7]	6[7]	3	13[3]
Order Hymenoptera						
Suborder Apocrita						
Ichneumonidae	7[7]	9[5]	6[5]	6[8]	10[5]	7[5]
Chalcidoidea	+	+	0	0	+	0
Order Araneida	0	1	+	1	0	1
Order Opiliones	+	+	0	1	+	1
Unidentified	1	1	2	1	2	2
Total occurrences	**800**	**602**	**735**	**811**	**754**	**881**
Total no droppings	**192**	**192**	**192**	**152**	**192**	**192**

Table 2.2. Percentage frequency of each food category in the samples of droppings pooled for each year at each site. +=<0.5%. [1-8]=rank of top 8 prey categories (based on data to 1d.p.).

The percentage frequency of each prey category at each locality pooled for each year is given in Table 2.2 and the pooled data have been combined across all localities/years in Figure 2.3. Eight major prey categories comprised over 75% of the combined diet: Tipulidae, Anisopodidae, Lepidoptera, Scatophagidae, Hemerobiidae, Ichneumonidae, Trichoptera and Calliphoridae/Muscidae. The major prey categories were similar across the four localities and three landscape types. Within the two lowland localities in England the same 8 major categories as above were represented, except where Empididae replaced Calliphoridae/Muscidae at Lowland A in 2004. A similar pattern was seen for the Welsh upland locality in 2005, except where Mycetophilidae replaced Calliphoridae/Muscidae. Within the high quality landscape in 2004, Calliphoridae/Muscidae and Trichoptera were absent from the major 8 prey categories, being replaced by Psocoptera and Mycetophilidae. Combining minor prey items present at less than 5 % into an 'other' category gives the following figures: Lowland A 2003 – 21 %, Lowland A 2004 – 27 %, Lowland A 2005 – 21 %, Lowland D 2003 – 18 %, High Quality B 2004 – 21 % and Upland C 2005 – 20 %.

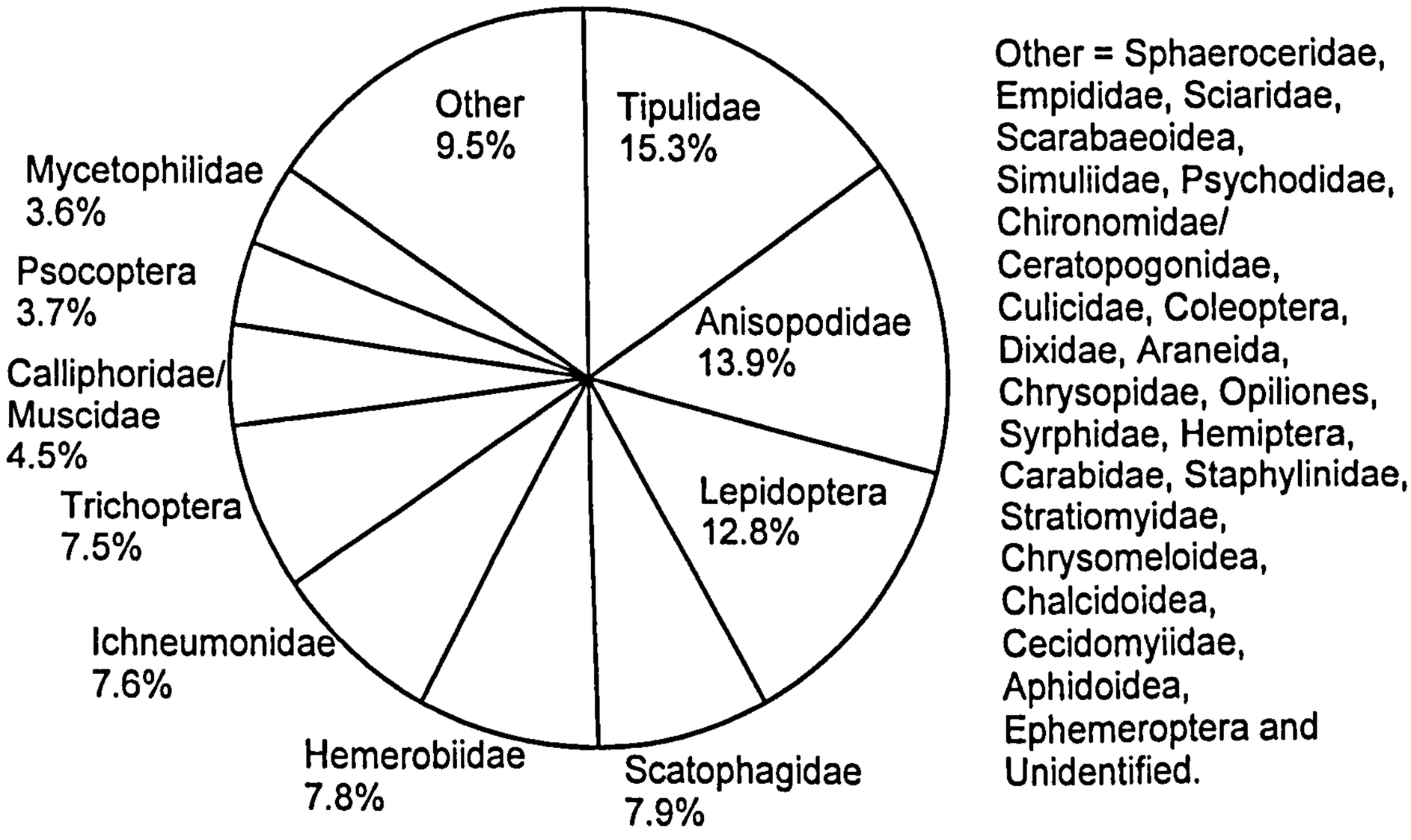

Figure 2.3. The percentage frequency of the prey categories in a total of 4583 occurrences in the 1112 faecal pellets analysed from all localities. The other categories occurred at <3%.

Geographical variation – sample data

In 2003, randomized contingency tables yielded bi-monthly significant differences in diet composition based on prey orders for sample 6 (late June) ($\chi^2 = 19.22$, d.f. = 4, $p < 0.001$). There were no significant differences between observed and expected values for prey orders in sample 6. Among families of Diptera, non-significant values were obtained for all samples.

In 2004, randomized contingency tables yielded bi-monthly significant differences in diet composition based on prey orders for sample 2 (late April) ($\chi^2 = 11.31$, d.f. = 2, $p < 0.01$). There were no significant differences between observed and expected values for prey orders in sample 2. Among families of Diptera, non-significant values were obtained for all samples.

In 2005, randomized contingency tables yielded bi-monthly significant differences in diet composition based on prey orders for sample 4 (late May) ($\chi^2 = 14.63$, d.f. = 4, $p < 0.01$). Significant deviations between observed and expected frequencies for individual orders were obtained for Trichoptera in sample 4 ($p < 0.01$), which was consumed exclusively by *R. hipposideros* in the upland landscape. Among families of Diptera, significant values were obtained for sample 1 (early April) ($\chi^2 = 22.25$, d.f. = 4, $p < 0.001$). There were significant deviations for Simuliidae ($p < 0.01$) in sample 1, which were eaten more frequently in the upland C landscape.

Seasonal variation

Significant seasonal variation in prey category is shown in Table 2.3 for each year at each locality. Consecutive pairs of samples have been combined to represent monthly samples (sample 1-2 = April; sample 3-4 = May; sample 5-6 = June; sample 7-8 = July; sample 9-10 = August; sample 11-12 = September). Several prey categories showed evidence of a consistent seasonal trend in occurrence. Psocoptera was largely absent from the diet in April and May and more often present later in the summer.

Prey category, roost and year	$p <$	April	May	June	July	August	September
Psocoptera							
Lowland A 2003	*0.05*	0	3	5	28	28	5
High Quality B 2004	0.01	3	0	50	34	41	22
Lowland A 2005	*0.05*	3	0	9	6	22	22
Upland C 2005	0.001	0	0	13	9	31	34
Hemerobiidae							
Lowland A 2003	0.01	47	47	56	44	9	0
Lowland D 2003	0.01	20	44	15	19	16	15
Upland C 2005	0.01	56	28	13	34	44	3
Tipulidae							
Lowland A 2003	0.01	72	91	100	66	22	19
Lowland D 2003	0.001	30	84	70	38	28	35
Lowland A 2004	0.01	41	59	81	50	22	16
Upland C 2005	*0.05*	50	97	100	88	63	91
Anisopodiae							
Lowland A 2003	*0.05*	50	38	63	69	94	47
Lowland D 2003	0.01	8	13	15	38	81	65
Lowland A 2004	0.001	41	25	44	34	100	97
High Quality B 2004	0.001	50	19	59	34	66	97
Mycetophilidae							
High Quality B 2004	*0.05*	28	13	31	0	31	22
Upland C 2005	0.001	78	41	9	16	6	16
Sciaridae							
Upland C 2005	*0.05*	25	28	9	3	6	6
Empididae							
Lowland A 2004	*0.05*	3	16	34	9	13	19
Sphaeroceridae							
High Quality B 2004	0.001	41	31	9	9	3	0
Calliphoridae/Muscidae							
Lowland A 2003	0.001	0	13	19	16	53	22
Lowland A 2004	*0.05*	3	9	6	16	28	25
Lowland A 2005	*0.05*	9	19	9	16	41	38
Scatophagidae							
Lowland A 2003	0.001	0	25	25	53	56	41
Lowland D 2003	0.01	4	22	15	28	78	70
Lowland A 2004	*0.05*	22	13	19	28	56	31
High Quality B 2004	0.001	9	3	38	34	72	66
Lowland A 2005	0.01	13	13	50	38	59	13
Upland C 2005	*0.05*	0	31	28	44	38	28
Lepidoptera							
Lowland A 2003	*0.05*	31	47	47	69	59	66
Lowland D 2003	0.001	10	47	98	100	50	90
Lowland A 2004	0.01	16	28	72	81	69	16
High Quality B 2004	*0.05*	16	50	66	88	69	28
Lowland A 2005	0.01	22	63	72	81	59	16
Upland C 2005	*0.05*	19	50	41	63	78	22
Trichoptera							
Lowland A 2003	0.001	84	56	28	24	9	22
Lowland D 2003	*0.05*	4	25	55	22	16	25
Lowland A 2004	0.001	59	59	16	16	9	6
Lowland A 2005	*0.05*	38	25	19	6	9	31
Ichneumonidae							
Lowland A 2004	0.01	16	66	34	50	31	9
High Quality B 2004	0.001	9	78	56	53	44	19

Table 2.3. Significant seasonal variation in prey category at $p<0.01$ and $p<0.001$ level. Values are expressed as percentage occurrence in the droppings. Variation at $p<0.05$ level is also shown.

Tipulidae in general demonstrated a peak in June, whereas the frequency of Anisopodidae generally increased through the summer and peaks in August and September. Scatophagidae and Calliphoridae/Muscidae exhibited a similar pattern. They were largely absent in the diet in April and May, increasing to a peak in August. Lepidoptera was generally more frequent in June, July and August, with a further peak in abundance in September in 2003. There was no consistent trend between lowland localities for Trichoptera but at the Lowland A roost it was most frequent in April and May, with a second smaller peak in abundance in September. I recorded the same pattern at the Upland C roost as well, although this was non-significant. Ichneumonidae reached a peak in abundance in May at both lowland and high quality landscapes in 2004.

To investigate seasonal variation further I combined samples for pre-parturition (samples 1-6) and post-parturition (samples 7-12) using prey categories. There was highly significant variation ($p < 0.001$) between pre- and post-parturition diet at each locality. However there was little consistency within individual prey categories and no prey category was constantly observed significantly more than expected in either the pre- or post-parturition diet for each locality. Scatophagidae was closest to a consistent trend. It was always observed less than expected in the pre-parturition diet and more than expected post-parturition, although differences were not significant for Lowland A in 2005 or Upland C in 2005.

Diet breadth

Diet breadth for the two localities studied each year are given in Figure 2.4. Shannon-Weiner indices were calculated using prey categories. There was no significant difference in the Shannon-Weiner diversity index value calculated using prey categories between localities (landscape types) and between samples in 2003 ($F_{1,10} = 0.004$, NS and $F_{10,10} = 0.506$, NS), 2004 ($F_{1,11} = 0.29$, NS and $F_{11,11} = 0.92$, NS), or 2005 ($F_{1,11} = 0.70$, NS and $F_{11,11} = 0.65$, NS).

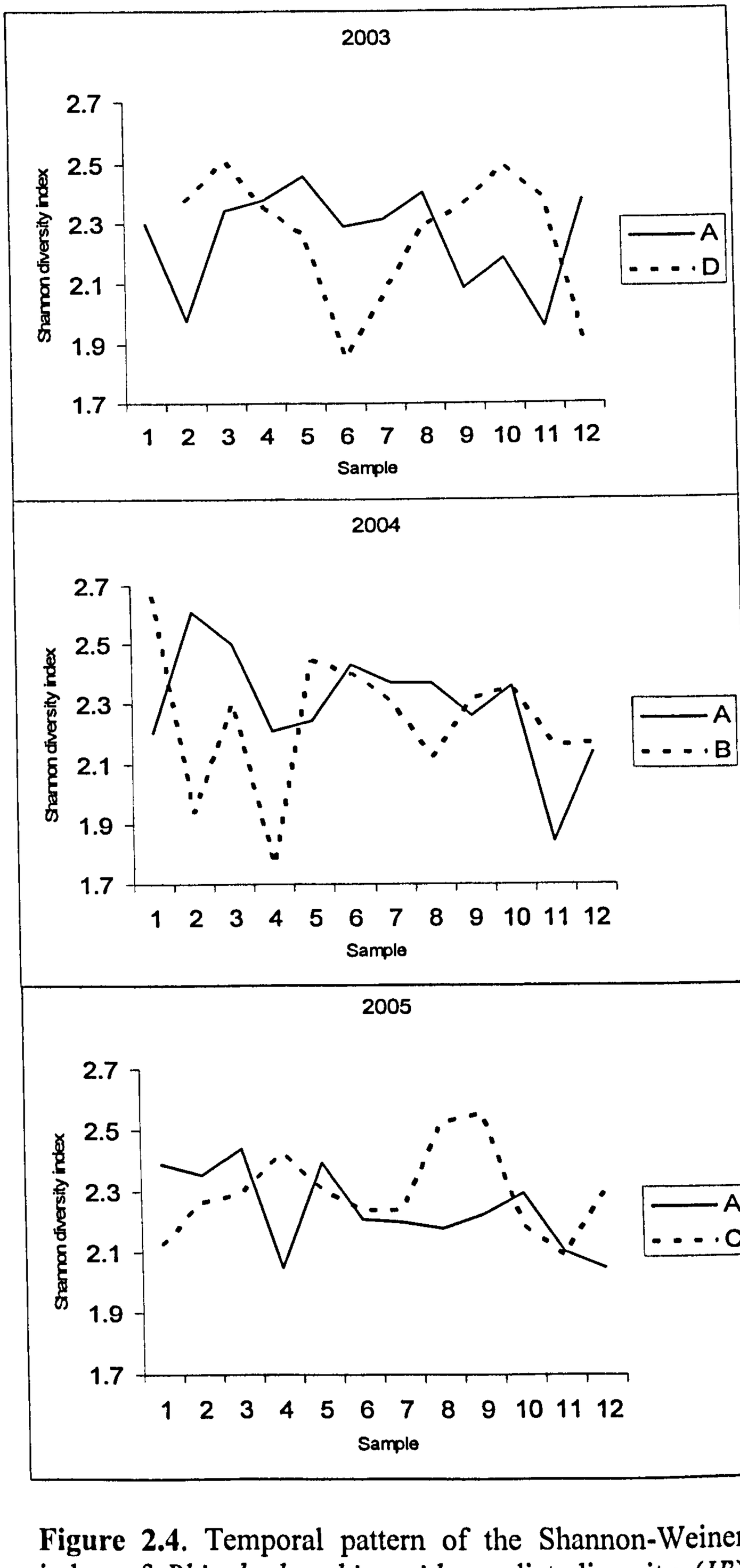

Figure 2.4. Temporal pattern of the Shannon-Weiner index of *Rhinolophus hipposideros* diet diversity (*H'*) during 2003-5 at locality lowland A, high quality B, upland C and lowland D.

Randomized contingency tables demonstrated significant seasonal variation in some prey categories within monthly samples. Consequently Shannon-Weiner diversity indices were also calculated using variations in prey categories within monthly samples. However there was no significant difference in the Shannon-Weiner diversity index value between localities (landscape types) nor between samples in 2003 (two-way ANOVA (without replication), $F_{1,5} = 0.16$, NS and $F_{5,5} = 0.46$, NS), 2004 ($F_{1,5} = 0.004$, NS and $F_{5,5} = 4.16$, $p = 0.07$, NS), or 2005 ($F_{1,5} = 1.16$, NS and $F_{5,5} = 1.38$, NS).

Comparison with previous studies

As detailed in the Introduction several previous studies on the diet of *R. hipposideros* have been undertaken. The findings were synthesized in a review of the diets of British bats (Vaughan 1997) and the summary table from this review is adapted in Table 2.4. It has been updated to incorporate both the findings of Arlettaz *et al.* (2000) and Williams (2001) in relation to the summer diet of *R. hipposideros*, and the present study to allow comparison between data. The results of the present study are listed as both percentage occurrence and percentage frequency to allow comparison with different authors. The data for the Lowland A roost for 2003, 2004 and 2005 have been combined.

Source	Location	Method	*n*	C.Ar.	Pso.	Hem.	Neu.	Col.	Dip.	Lep.	Tri.	Hym.
(Poulton 1929)	England	pr	?	✓					✓	✓✓		
(Leishman 1983)	England	fa, % o	55			2	36	9	80	89	31	35
(McAney and Fairley 1989)	Ireland	fa, % f	630	3		1	13	3	41	19	18	4
(Hollyfield 1993)	England	fa, % n	240			2	14		44	35	1	3
(Beck et al. 1989)	Switzerland	fa, % o	880		3	1	37	2	76	63		3
(Beck 1994-1995)	Switzerland	pr	11				✓	✓	✓			
(Arlettaz et al. 2000)	Switzerland	fa, %o	240		20		49	24	63	85	15	8
(Williams 2001)	England	fa, % f	?	2	1	1	10	3	52	16	6	9
Knight	England A	fa, % f	576	1	5	0	13	4	34	18	12	11
"	England D	fa, % f	152	3	5	1	11	2	33	26	10	9
"	England/Wales B	fa, % f	192	0	9	0	15	3	32	18	5	15
"	Wales C	fa, % f	192	2	5	0	10	2	33	15	20	11
"	England A	fa, % o	576	2	15	1	37	12	96	51	34	31
"	England D	fa, % o	152	6	11	1	22	5	68	55	20	18
"	England/Wales B	fa, % o	192	1	25	1	44	9	91	53	14	43
"	Wales C	fa, % o	192	5	15	0	30	5	97	45	59	33

Table 2.4. The diet of *Rhinolophus hipposideros.* Adapted from Vaughan, N. (1997) *Mammal Review*, **27**, p81.

Key to abbreviations in table:
Methods: pr, prey remains found under feeding perch or roost; fa, feacal analysis; %f, percentage frequency; %n, percentage numbers; %o percentage occurrence; *n*, number of pellets or prey remains; ?, data not available
Prey taxa: C.Ar., Class Arachnida; Pso., Psocoptera; Hem., Hemiptera; Neu., Neuroptera; Col., Coleoptera; Dip., Diptera; Lep., Lepidoptera; Tri., Trichoptera; Hym., Hymenoptera; ✓ = present in diet, ✓✓ = important in diet

2.5 *Discussion*

Faecal analysis has been shown to be a valid method to determine the diet of insectivorous bats (Kunz and Whitaker Jr. 1983) and permits non-destructive sampling. A disadvantage is the lack of data about differential digestion. However the problems associated with differential digestion may not be as serious in insectivorous bats as they are in other mammals because most food passes through the gut of bats rapidly and because most insects have hardened exoskeletons composed of protein and chitin (Kunz and Whitaker Jr. 1983). Digestion tends to destroy soft insect parts, for example Rabinowitz and Tuttle (1982) demonstrated that mayflies, a soft-bodied insect, can be under-represented in faecal analysis. Therefore faecal analysis can result in a bias toward less digestible, hard-bodied prey. Another major limitation of faecal anlysis is the inability to identify prey fragments to lower taxonomic level and in this study some prey was identified to order or sub-order level only. Hence variation in faecal composition within orders may be masked. A range of techniques have been developed for identifying prey remains at the molecular level, including using DNA-based methods (see review by Symondson (2002)) which could overcome the problem of species-level indentification of prey remains in bat faeces. Notwithstanding these limitations, comparisions between the faecal compositions of different samples can be made; although there is unlikely to be direct corresponce with the actual diet of the bats.

Although the diet of *R. hipposideros*, as determined by faecal analysis, was fairly consistent in terms of major prey categories consumed - Diptera (principally Tipulidae, Anisopodidae and Scatophagidae), Lepidoptera, Neuroptera (principally Hemerobiidae), Trichoptera and Hymenoptera (principally Ichneumonidae), and there was no difference in dietary breadth at the paired sites, the composition of the diets did differ significantly geographically.

The difference between two lowland localities (A and D in 2003) was significant at the $p < 0.01$ level, whereas the differences between lowland and high quality landscapes (A and B in 2004) and lowland and upland landscapes (A and C in 2005) were highly significant ($p < 0.001$). The diet of *R. hipposideros* in the Lowland A roost was found to be relatively more constant in each of the three

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years, except only in respect of abundance of Neuroptera. This is unsurprising as Owen (1991) has shown annual catches of Neuroptera fluctuated considerably from year to year.

In general terms the results of the present study are similar to those previously undertaken with the same prey orders recorded overall. The most consistent difference is that Psocoptera was absent from over half of the previous studies. It has previously been recorded in Switzerland (Beck et al. 1989) and in England (Williams 2001), but was constantly present and more abundant in the current study, in similar abundance to that recorded by Arlettaz *et al.* (2000).

Comparing the results of the present study with those of Leishman (1983) in England, and Beck *et al.* (1989) and Arlettaz *et al.* (2000) in Switzerland, shows that Diptera were more commonly recorded in the present study whereas Lepidoptera were less abundant. Trichoptera and Hymenoptera were either not recorded or present at low abundance in the two Swiss studies but their occurrence varied quite considerably in the present study, being particularly abundant in the Welsh upland landscape and England/Wales high quality landscape respectively. On average the results are similar to those in Leishman's study.

Diptera has probably been overestimated in the summary of McAney and Fairley's (1989) Irish study and Williams' (2001) study in England. I calculated the figures by summing over different Diptera categories (e.g. sub-orders or families) rather than calculating from the raw occurrence data, and as such comparisons are inconclusive. The values for Trichoptera in Ireland and Wales are similar, whereas this order was less abundant at English sites. Hymenoptera were generally more abundant in the present study.

Of the numerous dietary analysis studies have been undertaken on insectivorous bats, relatively few have considered spatial variation in diet. In general such studies indicate spatial differences are due to changes in prey availability specific to that locality. The variation in diet of *Antrozous pallidus* in California reflects prey availability and individual foraging behaviour (Johnston and Fenton 2001). Similarly Anthony and Kunz (1977) explain the variation in feeding habitats of

Myotis lucifugus as the species exploiting changes in the local insect fauna to the best advantage, whilst variation in Coleoptera in the diet of *Plecotus townsendii virginianus* might be related to differences in the proximity of open fields to the roost (Sample and Whitmore 1993).

Within my study, the greatest variation in abundance of a prey category between localities was shown by Trichoptera. All but one species of this family in Britain have aquatic larvae. Most pupate in the spring and emerge as adults in early summer, and newly emerged adults can be seen in large numbers over the water, often in small swarms (Chinery 1993). This seasonality agrees with my findings at the Lowland A and Upland C roosts. I recorded Trichoptera most frequently in April and May, with a second smaller peak in September, suggesting that in these localities *R. hipposideros* were preying on newly emerged Trichoptera in early summer. Adults are usually flying at dusk and smaller species rarely travel far from water, although larger ones, with stronger flight, often turn up in light traps some distance from water (Chinery 1993). However recent work by Petersen *et al.* (2004) found the local dispersal range of Trichoptera from the stream channel to be short, with half of individuals caught in Malaise traps with 7-11m of the stream channel. Therefore it seems likely that Trichoptera are generally caught close to water and the variation in abundance in Trichoptera across the localities can be explained by differences in landscape and habitat. Trichoptera was most abundant at the Upland C locality, which was characterised by numerous small streams that drain through the valleys from the higher moorland and generally feature continuous bankside tree cover. Lowland A landscape also featured a number of small brooks and streams. In contrast there were very few small streams present in the high quality landscape, and although the River Wye was a dominant feature it was unlikely to be used by foraging *R. hipposideros* due to its large size (width 40-45 m) and lack of continuous bank side tree cover.

Further evidence for landscape differences in diet is shown by the presence of Psocoptera in faeces. Although this order was recorded from faecal samples from all three landscapes at relatively low frequency there was a highly significant increase in abundance at the high quality landscape compared with the lowland. Psocids are small, rarely exceeding 6 mm in length but most outdoor species are

fully winged and can be found in large numbers (New 1974, Chinery 1993). They are generally arboreal tree-dwellers and their significance in the diet in the high quality landscape can be explained by the high proportion of woodland and tree cover compared with the other landscape types.

Maternity roosts of *R. hipposideros* are predominantly comprised of breeding females with smaller numbers of immature bats of both sexes from previous years and mature males. Male bats can comprise some 24-30% of individuals within a colony (Bontadina et al. 2002) (pers. obs.) so droppings that I collected were assumed to be from both sexes. Of the numerous faecal analysis studies that have been undertaken on insectivorous bats, few have studied differences according to sex. Adult male and female *Myotis velifer* consumed the same prey items, although males consumed smaller quantities of food (Kunz 1974). There were no significant differences between the diets of males and females in *Pipistrellus pipistrellus* (Swift et al. 1985) nor in either *Tylonycteris pachypus* or *T. robustula* (Zhang et al. 2005). Of particular relevance is the study of *R. hipposideros* by McAney and Fairley (1989) in Ireland that showed no apparent difference in the composition of faecal samples from maternity and male roosts. Therefore, assuming there are no sex differences in the diet of *R. hipposideros*, changes in diet composition through the breeding season were likely to be a reflection of changes in prey availability or changes in foraging strategy.

In terms of my data, significant differences between localities generally only occurred in April, May and June (samples 1-6), which correspond with the pre-parturition period for *R. hipposideros* (Gaisler 1966), suggesting that geographical variations were particularly noticeable prior to the birth of young. Although the pre- and post-parturition diets were significantly different for each locality studied, there was little consistency between variations in prey categories between the roosts. The nutritional status of individuals is one of the most important factors governing their survival and reproductive success (Metcalfe and Monaghan 2001). Although lactation is believed to be the energetically most demanding period in a yearly life cycle of a female bat (Speakman and Racey 1987, Kurta et al. 1989), it occurs at a time of maximum prey availability (Racey 1982, Racey and Entwistle

2000). In contrast, pregnancy coincides with a time of reduced food availability, low ambient temperatures and often poor foraging conditions.

Temperate bats of the family Rhinolophidae use delayed fertilisation and torpor to survive periods of poor food availability (Altringham 2003), and Reiter (2004b) showed that low temperatures in June may have resulted in delayed birth in *R. hipposideros* in Austria, and an extended period during which birth took place. As with sex differences, few have studied differences in diet according to reproductive status in females. There was no significant difference in diet composition between early pregnancy, late pregnancy, lactation and weaning in *Pipistrellus pipistrellus* (Swift et al. 1985), and no difference between lactating and non-lactating female *Tylonycteris pachypus* or *T. robustula* (Zhang et al. 2005). In contrast Agosta *et al.* (2003) found that during the pre-maternity period diet breadth of *Eptesicus fuscus* was narrow, reflecting specialisation on Coleoptera, and broadened abruptly at the onset of the maternity period. They also found a greater volume of larger beetles were eaten during the pre-maternity period. In *R. ferrumequinum,* dietary diversity during late pregnancy became greatly reduced due to the heavy dependence upon Lepidoptera, but was relatively unspecialised during early pregnancy and post-lactation (Jones 1990). Both Coleoptera and Lepidoptera are classed as nutrient-rich, profitable prey, and specialising on them during pregnancy may be a strategy for minimising time spent foraging while maximising energy intake (Jones 1990). Goiti *et al.* (2004) also found that moths and beetles were positively selected by *R. euryale* in the pre-breeding season. In addition Diptera other than Tipulidae were seldom consumed and they postulate that the higher profitability of tipulids among flies may be a consequence of their larger wingspan resulting in slower flight. It is likely then that *R. hipposideros* are selecting nutrient-rich, profitable prey where possible.

Animals will feed most efficiently if they accept all potential prey items encountered when prey is scarce but show greater selectivity as prey becomes abundant (Emlen 1966). Prey selection studies undertaken on *Rhinolophus* spp. have indicated both selective, for example *R. ferrumequinum* (Jones 1990) and *R. euryale* (Goiti et al. 2004), and unselective feeding, for example *R. rouxi* (Eckrich and Neuweiler 1988). McAney and Fairley (1989) suggest *R. hipposideros* may

forage unselectively, though no measurements of prey availability were made. Within my study there was a similar seasonal variation evident at each locality for some prey categories suggesting that *R. hipposideros* were taking prey according to availability. A study on availability of prey was not simultaneously attempted during the dietary analysis. Obtaining unbiased measures of insect availability are not currently possible (Kunz 1988, Whitaker 1994). In particular *R. hipposideros* exhibit a number of feeding strategies such as aerial hawking and gleaning (Jones and Rayner 1989) and foraging both over a wide area and in a range of different habitat types (Bontadina et al. 2002). Designing a suitable insect sampling strategy is therefore effectively impossible.

Rhinolophids use long constant frequency (CF) components in their echolocation calls, initiating and terminating with brief frequency modulated (FM) sweeps. For *R. hipposideros* the CF component of the echolocation calls is close to 112 kHz (Kay and Pickvance 1963, Jones and Rayner 1989), with a wavelength of 2.94 mm. This call structure allows rhinolophids to discriminate between different kinds of prey in cluttered environments (Emde and Menne 1989, Jones and Rayner 1989, Emde and Schnitzler 1990), which is consistent with selective feeding, as shown by *R. ferrumequinum* and *R. euryale*. Morphologically however *R. hipposideros* is quite different from *R. ferrumequinum* and *R. euryale* as it has low body mass, low aspect ratio, low wing loading and relatively low flight speed. Aldridge and Rautenbach (1987) found that such bats were characterised by high manoeuvrability and ability to forage in cluttered environments. They postulated that bats such as *Hipposideros caffer*, with lower flight speeds (low mass, low wing loading and low aspect ratio) have to fly in environments which support high insect densities, typically cluttered habitats, in order to maintain a positive energy budget and minimise foraging time. They further surmise that species that appear to be adapted primarily for manoeuvrable flight in clutter may be able to reduce foraging flight costs, without increasing foraging time and decreasing insect encounter rates, by flying in insect concentrations that form outside cluttered areas, for example insect swarms.

Swarming consists of a quasi-stationary flight over a landmark, often undertaken by many individuals together (Downes 1969). The landmark is usually a more or

less conspicuous element in the landscape such as a road, a treetop, below the tip of a branch, in an opening of a woodland canopy, above a cow, cow dung, an outstanding leaf (see review by Downes (1969)). Many of the families of Nematocera found in the diet of *R. hipposideros* in this study (smaller species of Tipulidae/Trichoceridae, Anisopodidae, Culicidae, Dixidae, Psychodidae and Chironomidae/ Ceratopognidae) are known to exhibit swarming behaviour. In addition Trichoptera and Spahaeoroceridae also swarm. They are active at dusk or during the night, showing a gradual increase in activity after dusk which ceases quickly late in the night with a further marked peak in activity around dawn (Lewis and Taylor 1964, Colyer and Hammond 1968, Skidmore 1991, Peng et al. 1992b, Chinery 1993). Adult Neuroptera, although not known to swarm, are also mainly active at dawn and dusk (Tilling 1987). Scatophagidae, although essentially diurnal (Parker 1970), are also active early in the night, up to 0.75-1.5 h after sunset (Williams 1935). Together these prey categories comprise 54-60 % of the diet in terms of frequency (within pooled data). Whilst the presence of non-volant prey in the diet, such as spiders and caterpillars, confirms that *R. hipposideros* use gleaning as a foraging technique, volant prey could potentially be caught either on the wing during aerial hawking, for example within swarms associated with trees, or while at rest on vegetation by gleaning. Their long duration CF calls means *Rhinolophus* species can detect fluttering targets among echo clutter as echoes from moving insect wings contain abrupt changes in frequency and intensity wherever the wing position is normal to the sound beam (Neuweiler 1989). Therefore their specialised echolocation suggests that gleaning is unlikely to be the principal foraging strategy with the majority of prey caught on the wing during aerial hawking. Given the large proportion of swarming insects in the feacal composition, feeding on swarming insects could play an important part in foraging. This shall be discussed futher in light of the results from the radio-tracking study in Chapter 3.

Implications for conservation

Scatophagidae was one of the major prey categories in the diet. The larvae of the yellow dung-fly *Scatophaga stercoraria* develop in cattle dung. The use of antihelminthic drugs in cattle and sheep to kill internal parasites is widespread and

low concentrations of the drug ivermectin can have severe effects in the abundance of *Scatophaga stercoraria* (Strong 1993). 50 % of *Scatophaga stercoraria* were killed within 48 hours of exposure to ivermectin at a concentration found in cattle dung treated with an ivermectin slow-release bolus (Strong and James 1992). Levels similar to that in cow pats from injected animals debilitated larvae, which sometimes failed to mature, and caused deformities in the wings of adults. However sustained-release boluses are primarily used in first year grazing animals with systemic used in second summer if they have not calved, thus only a proportion of dung would be affected. Until the likely impact of this on *R. hipposideros* has been evaluated further it may be advisable to avoid the use of avermectins around maternity roosts.

CHAPTER THREE

FORAGING AND COMMUTING BEHAVIOUR OF *R. HIPPOSIDEROS*

3 Foraging and commuting behaviour of *R. hipposideros*

3.1 *Summary*

I examined the behaviour of *R. hipposideros* by using radio-tracking in three counties of England and Wales. The localities represented three different landscape types: lowland, upland, and a landscape considered to be of high quality for the species. In total, I analysed 3374 tracking fixes collected for 54 individuals during a period of three years (2003-5).

The behaviour of *R. hipposideros* was consistent across the three landscapes, despite the high quality roost supporting over four times as many bats. Average range was 2 km and home range was 147-177 ha. I postulate that the bats were adopting an optimal behaviour that is constrained by the species' morphology, regardless of the surrounding landscape.

The bats foraged within or close to the tree canopy. Bats flew for on average 57 % of the night, with lactating females flying for significantly longer. The bats displayed multimodal flight activity, with the first flying bout being longest, agreeing partly with my earlier predictions that dusk and dawn were important foraging times for *R. hipposideros* (refer to Chapter 2). Emergence timing in the upland landscape was earlier than previously recorded in other studies thus enabling the colony to begin foraging before the abundance of prey declined. The first flying bout was significantly longer in the lowland landscape implying that feeding is more efficient in the high quality and upland landscapes, in accordance with optimum foraging models.

Colder temperatures and increasing rainfall actually resulted in bats flying for longer than usual, presumably due to reduced quality of foraging, whereas wind speed affected *R. hipposideros* differently at different stages of the breeding cycle.

3.2 *Introduction*

Over the last two decades radio-tracking has been used successfully to study the ecology of many species of Chiroptera (see review by Fenton (2003)). Until recently the high mass of transmitters prevented their use on low-mass species because the transmitters would exceed the recommended limits of justifiable increased weight (Aldridge and Brigham 1988). However advances in radio-tag technology have led to the miniaturisation of transmitters and studies are beginning to focus on smaller species (Davidson-Watts and Jones 2006, Davidson-Watts et al. 2006).

R. hipposideros is one of Europe's smallest and rarest bat species and is now virtually extinct in large areas of north-west Europe (Stebbings and Griffith 1986, Stebbings 1988, Ohlendorf 1997). The species is protected by law in Britain and in the European Union. It is a Priority Species under the UK Biodiversity Action Plan (Anon 1995) and is also covered by the Agreement on the Conservation of Populations of European Bats (UNEP/EUROBATS) (1991), both of which state the need to identify and protect important feeding areas for *R. hipposideros*. Identification of sustenance zones around maternity roosts has been fundamental to the development of guidelines for protection of feeding areas for other species of conservation concern, for example *R. ferrumequinum* (Duvergé and Jones 1994, Jones et al. 1995, Duvergé and Jones 2003) and *Myotis nattereri* (Smith and Racey 2002), and can make a vital contribution to securing long-term favourable conservation status.

Earlier studies into the foraging activity of *R. hipposideros* involved use of ultrasound bat detectors (McAney and Fairley 1988b) or light tagging (Schofield 1996). More recently radio-tracking has overcome the limitations of this early research on the species and a number of studies have been undertaken (Stebbings 2000, Billington 2001, 2002, Bontadina et al. 2002, Holzhaider et al. 2002, Motte and Libois 2002, Schofield et al. 2002, Billington 2003, Smith and Morgan 2003, Andrew McCarthy Associates 2004, Cresswell Associates 2004, Billington and Rawlinson 2006, Smith 2006). The earlier studies are reviewed in Chapter 1 with relevant data (where provided) summarised in Table 1.1. The majority of these

studies were limited by time and budget constraints and most are characterised by small sample sizes. Consequentially there was a need to undertake a more systematic, extensive study to further inform conservation planning. To formulate management plans and target limited resources most effectively it is important to determine parameters that describe foraging behaviour. For example the maximum and mean range that bats are recorded away from the maternity roost allows identification of sustenance zones and how bats commute to foraging sites has implications for flight lines and connectivity between feeding patches.

In Chapter 2 I determined that there were geographoical variations in the diet of *R. hipposideros* as determined by faecal analysis, with differences between the lowland and high quality landscapes, and the lowland and upland landscapes in particular highly significant. Spatial differences are likely to be due to changes in prey availability specific to the locality and I related the differences to habitat variation. Therefore given significant variation in faecal composition, does foraging strategy also vary? In accordance with optimum foraging model, poor habitat quality would result in animals spending longer to forage and/or using larger foraging areas (Stephens and Krebs 1986). Thus I hypothesise that spatial variation in foraging behaviour exists. Range sizes, as well as foraging times, could be expected to be also greater in bats with higher energy demands, such as during lactation, energetically the most demanding period in a yearly life cycle of a female bat (Speakman and Racey 1987, Kurta et al. 1989). Hence I also hypothesise that foraging behaviour would also vary according to reproductive status. Any such variations need to be investigated so that mangament plans are effective across the range of *R. hipposideros* in Britain.

I undertook a large-scale radio-tracking study to investigate the foraging and commuting behaviour of *R. hipposideros* within three distinct landscape types in Britain and to determine whether spatial and seasonal variation exists.

The specific aims of this chapter are:

1. To determine parameters that describe foraging behaviour, such as emergence timing, proportion of night time spent flying, home range size, overlap between ranges, foraging density.

2. To describe commuting behaviour and investigate possible barriers to commuting.
3. To test the hypothesis that behaviour varies across different landscape types in Britain.
4. To test the hypothesis that behaviour varies according to reproductive status.
5. To describe any similarities between my study and previous research into the behaviour of *R. hipposideros.*
6. To investigate the link between foraging behaviour and the results of the diet study in Chapter 2.

3.3 *Methods*

3.3.1 *Study sites, capture of bats and tagging procedure*

The radio-tracking study of *R. hipposideros* was conducted during the summers of 2003, 2004 and 2005. I undertook all of the fieldwork including the radio-tracking. Bats were sampled from three maternity roosts representing the key landscape types that characterise the distribution of *R. hipposideros* in Britain: lowland (Roost A, North Somerset), a high quality landscape (Roost B, Wye Valley, Gloucestershire and Monmouthshire) and upland (Roost C, Powys). For descriptions of study sites refer to Section 2.3.1, Chapter 2. The study was conducted during early to late May (early pregnancy), late May to early June (late pregnancy), late July to mid-August (lactation) and late August to mid-September (post-lactation). Bats were radio-tracked from High Quality B in 2004 and Upland C in 2005. To allow comparison between data and the assessment of the foraging behaviour within a lowland landscape more fully, Lowland A was studied in all three years.

To minimise disturbance to the colony, bats were caught in a static hand net at one of the roost entrances as they emerged at dusk except for 13% of individuals (n = 18 of 139), which were caught in the roost as it was not possible to use a hand net at the entrance. After capture, bats were held in catch bags before biometric data were obtained. Individuals were sexed and the breeding status of females assessed

by checking for pelvic nipples (Gaisler 1963b). Bats were assigned to an age class, defined as juvenile (yearlings with grey fur and lacking ossification of the epiphyseal joints in the finger bones (Anthony 1988)), nulliparous females (females lacking pelvic nipples) or adult (parous females with pelvic nipples). Forearm length was recorded using plastic callipers (Moore & Wright, Hampshire, UK) to 0.1 mm. Body mass was recorded by weighing bats in a small plastic bag with a Pesola (Baar, Switzerland) Micro-Line 30 g scale to 0.1 g. Between two and six bats were then selected per session for radio tagging. To meet the objectives and avoid small sample sizes emphasis was placed on studying female bats and any males caught were disregarded unless juvenile. Larger bats were selected to minimise risk of adverse effects of carrying extra weight, using forearm length as a measure of skeletal size, following Bontadina *et al.* (2002).

Lightweight radio transmitters (<0.35 g PIP3 single celled tag) from Biotrack Ltd. (Wareham, UK) were used. The transmitter batteries had a life of between five and sixteen days. The fur between the scapulae was clipped using cuticle scissors and the tag was glued to the skin using Skinbond surgical contact cement (Smith & Nephew United Inc., supplied by Alana Ecology Ltd., Shropshire, UK). The transmitter remained attached to the bat for a maximum of two to three weeks although in May the transmitters sometimes fell off after just one week, presumably when the bats were moulting. Tagged bats were ringed using 2.9 mm magnesium-aluminium flanged rings (Mammal Society, London, UK). Only tagged bats were ringed to enable identification of tagged individuals in subsequent years of the project, to avoid re-tagging the same individual. Captured bats were then released outside the roost, adjacent to the principal commuting route away from the roost.

3.3.2 *Radio-tracking equipment and data collection*

Bats were located after release using a Lotek Suretrack STR_1000 receiver (Lotek Wireless Inc., Newmarket, Canada) connected to either a hand-held directional three-element Yagi aerial or a magnetic whip aerial attached to the car roof (aerials supplied by Biotrack Ltd., Wareham, UK). As in studies on other species of Rhinolophidae, continuous tracking was undertaken (Russo et al. 2002, Duvergé

and Jones 2003) and locations were recorded at 5 min intervals using trigger signals from a Casio Auto EL LCD watch whilst the bats were active. Continuous tracking was most suited to the project given the constraints of a short battery life meaning that discontinuous tracking with locations recorded at >15 min intervals would yield too few locational fixes (Harris et al. 1990). It was not possible to undertake triangulation, whereby two field workers co-ordinate simultaneous bearings (Kenward 2001), due to lack of sufficient manpower and field equipment. Therefore the 'close-approach' or 'homing-in' method (White and Garrott 1990, Kenward 2001) was applied: establishing the bat's position by approaching the subject tracked as close as possible by car or on foot. Kenward (2001) indicates that this is the best method for tracking moving animals and gives a reasonably accurate location with reference to landscape features rather than by plotting triangulation bearings. Locations were recorded using a Garmin GPSmap76 Global Positioning System (GPS) unit (minimum accuracy ± 10 m). Where close approach was not possible due to lack of access, bearings were taken using a prismatic compass and distance to the bat was estimated from the minimum signal strength, knowledge of the terrain and observer experience (O'Donnell 2000). Distance estimation was checked by using a transmitter placed in the field at known distances from the observer in different terrains. The range of the transmitters was between 0.2 km and *c.* 1.5 km. The confidence in the location was noted by assigning 1 of 3 accuracy classes (10 m, 50 m or 100 m). The highest accuracy class could only be assigned when I was in very close proximity to the bat and could either establish visual contact or signals were very strong, even at the lowest gain and volume setting on the receiver and non-directional. Each determined or estimated location of the bat (hereafter termed a fix) was recorded as a six-figure grid reference (±100 m). If there was poor resolution of a fix (signal classified as very faint i.e. high gain or direction uncertain e.g. due to signal bounce) then I omitted the fix from the analysis. Although bats were followed continuously, and locations were recorded every 5 min, analysis was undertaken using fixes recorded at 15 min intervals to minimise the autocorrelation of data. Sub-sampling within field data to avoid autocorrelation may provide so few locations that range sizes are underestimates (Kenward 2001). Therefore Harris *et al.* (1990) recommend that the radio-tracking regime is designed to collect locational fixes in a manner that minimizes the effects of autocorrelation as far as

possible. The flight speed of *R. hipposideros* at foraging sites has been recorded using multiple flash photography as 3.5 ms^{-1} (Jones 1993, Jones and Rydell 1994) so theoretically the species could cross 3.15 km in 15 min. In the field radio-tracked bats were timed between roosting sites and foraging areas where possible, and were found able to cross their range in <15 min.

An activity category was also assigned depending on the signal variation and location of the animal: commuting (rapid, directional movements between distant sites), foraging (sustained activity within a defined area of variable size), perching (typically a period of inactivity <10 min where the bat was hanging from a tree), night roosting (typically a period of inactivity >10 min within a building) or day roosting.

On the first night that the bats were tagged contact was maintained with all tagged bats where possible, although these data were omitted from the analysis. This gave the bats time to settle after the tagging procedure and minimised the risk of recording atypical behaviour as a possible reaction to being tagged. Subsequently, each night in succession one individual bat was followed to compile full nights' data per bat. Occasionally, where tagged bats were close to one another I could monitor two or more bats at once by alternating between the frequencies.

Details of any observed behaviour of the bats, including non-tagged bats from the colony, were recorded throughout. In addition the following weather conditions were recorded at dusk and dawn and at hourly intervals in between: air temperature (^{o}C), wind speed (Beaufort scale), wind direction, rainfall (ranked descriptively as 0 = none, 1 = spots, 2 = drizzle, 3 = fine, 4 = moderate, 5 = heavy, 6 = torrential), cloud cover (increments of 5 %) and moon phase.

3.3.3 *Data analysis*

Time, observer location, bearings, minimum signal strength, accuracy and activity class and general observations were recorded in the field on data sheets, and the determined or estimated locations displayed with the geographical information system (GIS) programme ArcView GIS 3.2 (Environmental Systems Research

Institute, Inc.). Base maps (Ordnance Survey Land-Line.Plus, multi-scale) were obtained from Digimap (© Crown Copyright Ordnance Survey, EDINA Digimap/JISC) and converted for use in ArcView with Map Manager (Environmental Systems Research Institute, Inc.).

The 'study area' is defined as a maximum range circle (MRC) centred on the roost site, containing all of the fixes of the radio-tracked bats from the colony. 'Home range' is defined as consisting of a more or less restricted area within which an animal moves when performing its normal activities (Harris et al. 1990). Given the limited battery life of the transmitters and that radio-tracking per individual was limited to just one part of the breeding season for each bat (e.g. lactation) the home ranges are considered seasonal and cannot be expected to describe the annual range requirements of the study animals (Harris et al. 1990). However, my methods do allow a reasonable estimate of the home range used by the individual in the short term (Kenward 2001).

Home-range analyses were undertaken using the Ranges 6 v1.2 (Kenward et al. 2003) and Ranges 7 v1.0 analysis system (South and Kenward 2006) (Anatrack Ltd., Wareham, UK). To reduce potential problems of autocorrelation (Swihart and Slade 1985) I only used fixes recorded at 15 min intervals (as described in Section 3.3.2). An important assumption of probabalistic methods is independence (Harris et al. 1990), which although minimised in the study design could not be ruled out. Therefore I used non-parametric techniques that make no assumptions about the underlying distribution of fixes. Overall home ranges were calculated as 100 % minimum convex polygons (MCPs) (Mohr 1947) of all locations to allow comparison with other studies as recommended by Harris *et al.* (1990). Overall range span was calculated from the maximum width of the 100 % MCPs and overall maximum distance calculated as the distance of the furthest fix away from the maternity roost.

Harris *et al.* (1990) recommend using more than one method of home range analysis to provide information on the pattern of space use by an animal. Therefore in addition to 100 % MCPs, I used cluster analysis (Kenward 1987, 2001) to remove outlying fixes (usually day roosting and commuting fixes) and

hence describe core areas (Harris et al. 1990) of activity (usually comprising foraging and night roosting fixes). My field observations suggested that the tagged animals were using distinct core areas. I chose to use cluster analysis as it tends to be more accurate than harmonic mean contouring, with distinct cores being more easily determined and less variable in size than those derived by harmonic mean analysis (Kenward 1987). The proportion of the home range that could be defined as a core area was determined by plotting fixes against range size on a utilisation plot using cluster polygons. The inflexion point on the curve indicated that up to 15 % of fixes from each bat were used for excursive activity and increased the range size disproportionately. Therefore, 85 % cluster cores were used to assess 'core home range'. Core clusters often remain separate at this point and so cluster analysis can also identify patchiness in range use, for instance when the study animal forages in several separate areas (Kenward et al. 2003). Hence, the number of nuclei, that is the number of separate groups of fixes, within the 85 % cluster core was also recorded.

Interaction between animals was studied using the static interaction of overlapping home ranges recorded during a similar time period (Kenward 2001). *a/A* was used as a measure of the overlap, where a home range of area *A* has an area *a* overlapped by another animal. For each individual the mean of overlaps with all other individuals within the same reproductive class was used. Overlap matrices were created using both 100 % MCPs and 85 % cluster cores.

The estimation of foraging density was calculated based on the utilisation density of the radio-tracking fixes, following Bontadina *et al.* (2002). The utilisation density was determined using the proportion of fixes occurring within 100 m, 200 m, 300m, ... (up to the maximum distance recorded) radius around the maternity roost, multiplied by the assumed total number of bats occurring in the colony. This gave an estimated number of bats occurring within 100 m, 200 m, 300 m, ... radius of the roost, and was used to calculate the density of bats within each zone.

The utilisation distributions were used to generate random locations at the lowland landscape. The maximum range circle was sub-divided into concentric rings of 500 m radii and random fixes (2124 in total) were generated using a uniform

distribution within each ring using the Animal Movement SA v2.04beta Extension (Hooge and Eichenlaub 1997) in ArcView GIS 3.2. The generated random point distribution was then compared to the actual distribution of radio-tracking fixes to assess potential barriers to commuting.

Patterns of the distribution of fixes in relation to main roads were analysed using circular statistics (Batschelet 1981, Zar 1999). Two-way analysis of variance (ANOVA) and non-parametric Kruskal-Wallis one-way analysis of variance *H*-tests were used to initially analyse whether there were differences in behaviour between years among different reproductive groups at the lowland locality (Dytham 1999). General Linear Modelling (GLM) was then used to analyse the radio-tracking data. The following response variables were tested: mean emergence time in relation to sunset, mean return time in relation to sunrise, mean flying time, mean number of flying bouts per night, mean length of average foraging bout, mean length of first foraging bout, mean 100 % MCPs (nightly and overall), mean 85 % core (nightly and overall), mean range span, mean maximum distance travelled in a night and home range overlap. Explanatory variables were breeding status and locality (categorical variables) and, temperature and cloud cover at emergence, temperature and cloud cover at return, minimum night temperature, average nightly rainfall and average nightly wind speed (continuous variables).

The model simplification process using the GLM approach as advocated by Grafen and Hails (2002) was employed to reduce multiplicity of *p*-values. I focussed on explanatory variables that were of primary interest. The categorical variables were dictated by the experimental design whereas continuous variables were selected based on previous studies. Air temperature affects bat activity (Walsh et al. 1995) whereas wind speed, moon phase and cloud cover has no discernable effect (Vaughan et al. 1997). However my field observations suggested that cloud cover may affect emergence and return times, and rainfall and wind speed may affect foraging behaviour so these were included.

The assumptions of the GLM (independence, homogeneity of variance, normality of error and linearity/additivity) were tested using histograms of residuals, normal

probability plots and plots of standardised residuals against the fitted values/continuous variables, and transformations (square root, natural log and inverse) used where required. Multiple comparisons among the means of significant categorical explanatory variables were undertaken using Tukey's method. To avoid pseudoreplication only one data point per bat was used, that being the mean value of the response variable over the number of nights that the bat was tracked (refer to Table 3.1). All statistical analyses were carried out on Minitab version 13.32 for Windows (Minitab, Coventry, UK) with a significance level of 5 %.

3.4 *Results*

During the three-year study (2003-5) 57 *R. hipposideros* were fitted with radio-transmitters (refer to Appendix 1 for details). However, 3 individuals have been omitted from the analysis because either the transmitter failed or it was shed by the bat before sufficient data had been collected. In total 3374 fixes were used in the analysis, of which 25 % were assigned accuracy class 1 (10 m), 34 % accuracy class 2 (50 m) and 41 % accuracy class 3 (100 m). 2918 fixes were recorded in 145 full nights' data on the 54 individuals analysed. Plots of range size *vs.* number of fixes reached an asymptote for the majority of bats (50 out of 54) included in the analysis. Of the four bats that did not reach an asymptote 3 were juveniles, despite there being in excess of 95 fixes for each. The other was an adult female that had reached an asymptote but the tag was subsequently recovered off the bat in a roost outside of the recorded home range. Therefore range sizes may be more appropriately classified as minimum values, giving a snap-shot of bats behaviour at a certain time.

Sampling effort

The sampling effort is shown in Table 3.1. Effort was concentrated at the lowland landscape which was surveyed over the three summers. Here, bats were caught rarely in any one season so the age and sex class radio-tagged depended on the composition of the bats caught. However over the three years an equal sample from each reproductive class was obtained. Samples for nulliparous females in

the lowland landscape were too small to separate into different time periods. Due to the short life span of the transmitters bats were followed for relatively short periods (2.7±1.1, range 1-6 full nights' data), but sampling effort was similar for each reproductive class and landscape. Two-way ANOVA with replication showed that the mean number of fixes per bat did not vary significantly among reproductive classes ($F_{3,36} = 2.75$, NS) or landscape ($F_{2,36} = 1.85$, NS). A Sheirer-Ray-Hare test showed that the number of full nights' data per bat also did not vary significantly among reproductive classes ($p = 0.09$) or landscape ($p = 0.5$). Finally, analysis of variance showed that between localities bats were radio-tracked on similar dates (using Julian days) ($F_{2,142} = 0.119$, NS), and so any differences among sites are unlikely to be the result of differences in the timing of tracking.

	N			Mean total number of fixes per bat (± 1 SD)			Mean number of full nights' data (± 1 SD)		
	Lowland	High quality	Upland	Lowland	High quality	Upland	Lowland	High quality	Upland
Adult female									
Early pregnancy	6			36.2±8.6			2.3±0.5		
Late pregnancy	6	3	3	57.7±28.5	54.0±32.1	59.3±28.5	3.2±1.5	3.3±1.5	3.0±1.0
Lactation	6	3	3	57.0±29.7	63.7±13.7	66.0±33.7	2.8±1.7	2.7±0.6	2.0±1.0
Post-lactation	6	3	3	43.0±24.7	73.0±2.0	100.7±23.2	1.7±0.8	2.3±0.6	3.0±0.0
Nulliparous female	6			59.8±25.9			2.7±1.0		
Juvenile									
Female	2			99.0±7.1			3.0±1.4		
Male	4			101.0±16.7			3.5±1.3		
Totals	36	9	9	59.0±29.8	63.6±19.3	75.3±31.5	2.7±1.2	2.8±1.0	2.7±0.9
Overall total		54			62.5±28.8			2.7±1.1	

Table 3.1. Sampling effort for *Rhinolophus hipposideros* radio-tracked during summers of 2003-5 in three different landscape types in Britain.

Effects of year at lowland locality

Range statistics (100 % MCP, 85 % core, mean range, maximum range and range span) did not vary significantly between juvenile females and juvenile males among years (two-way ANOVA, $p > 0.05$). Similarly the range statistics did not vary significantly between years for nulliparous females or adult female sub-groups (categorised as early pregnancy, late pregnancy, lactation or post-lactation) so data were combined for these classes in analyses of ranges.

Means of behaviour parameters at each locality throughout the breeding season are provided in Table 3.2a and Table 3.2b. To allow further comparison between landscapes the overall means for adult females at each locality are given in Table 3.3.

Emergence behaviour

Emergence time (log transformed) varied significantly between landscapes (GLM, $F_{2,44} = 12.52$, $p < 0.001$). Overall, the time of emergence of *R. hipposideros* from the roost was very similar in the lowland and high quality landscapes (30 and 31 min after sunset respectively) but in the upland landscape the bats emerged just 14 min after sunset. Multiple comparisons using Tukey's method for locality indicate that the mean emergence time at the lowland and high quality landscapes were not significantly different but that bats emerged significantly earlier at the upland site compared with both others. Time of emergence was not affected by breeding status (GLM, $F_{5,44} = 2.33$, $p = 0.058$) or temperature (GLM, $F_{1,44} = 1.19$, NS). Interaction terms and cloud cover were removed during model simplification.

Variable	Early Pregnancy	Late Pregnancy	Lactation	Post-Lactation	Nulli-parous	Juvenile
Emergence (min after sunset)	27±12.1	35±3.5	28±4.8	35±19.5	33±11.8	28±6.7
Final return (min before sunrise)	31±6.6	37±5.5	34±5.3	37±8.0	36±5.4	31±7.8
Total night time from emergence to final return (min)	446±33.2	386±16.3	448±23.2	494±15.5	506±81.7	527±48.1
Overall flying time (min)	240±80.4	254±57.5	282±61.5	258±62.9	269±96.5	317±78.5
% overall flying time of total night time	54±18.7	66±12.7	63±13.1	52±13.8	53±16.5	60±15.6
No. of flying bouts	2.6±0.7	3.1±0.7	3.5±0.9	4.8±1.0	3.8±0.8	3.8±0.7
Average length of flying bout (min)	101±44.2	91±38.8	91±25.4	57±14.0	76±19.8	93±37.1
Length of first flying bout (min)	110±60.4	107±58.8	128±51.8	62±28.5	82±38	90±25.8
Length of last flying bout (min)	54±38.8	88±25.4	62±47.8	47±20.1	80±32.8	100±61.3
Length of all other bouts (min)	69±53.8	43±29.3	44±24.9	62±27.5	56±36.9	69±21.5
Overall 100% MCP (ha)	213±143.6	130±70.3	187±159.1	178±172.8	168±193.8	261±264.1
Overall 85% core (ha)	56±44.8	30±23.0	36±34.1	33±29.3	30±16.8	37±26.9
% overall core of MCP	28±12.8	22±11.8	28±18.9	22±13.5	30±17.0	26.3±19.9
Nightly 100% MCP (ha)	145±126.2	69±42.1	114±96.8	98±96.2	100±114.9	86±68.6
Nightly 85% core (ha)	27±14.2	20±16.8	23±14.7	25±16.9	22±14.2	23±17.7
% nightly core of MCP	29±12.0	32±16.4	31±15.1	37±20.8	39±24.3	35±10.3
Overall maximum range (km)	2.2±1.1	1.7±0.8	2.0±1.5	2.0±1.0	1.9±1.5	1.9±1.3
Overall mean range span (km)	2.3±1.1	2.0±0.8	2.2±1.5	2.2±1.1	2.0±1.6	2.2±1.3
Nightly range span (km)	2.0±1.0	1.5±0.8	1.8±1.2	1.4±0.9	1.5±1.3	1.4±0.9
Distance travelled per night (km)	6.3±2.1	5.3±1.6	7.2±4.0	6.5±3.6	5.6±3.6	6.7±3.3

Table 3.2a. Summary of the flight data for *Rhinolophus hipposideros* within the lowland landscape. Sample sizes are provided in Table 3.1.

Variable	Late Pregnancy	Lactation	Post-Lactation
Emergence (min after sunset)	33±3.0	21±7.3	37±21.1
Final return to roost (min before sunrise)	36±2.9	31±10.2	26±6.7
Total night time from emergence to final return time (min)	374±3.2	445±18.6	591±24.3
Overall flying time (min)	176±30.2	302±33.5	347±45.9
% overall flying time of total night time	47±8.3	68±6.1	58±5.9
Number of flying bouts	3.6±1.0	3.6±0.7	5.5±2.2
Average length of flying bout (min)	54±20.1	87±18.6	69±20.0
Length of first flying bout (min)	61±28.5	77±31.3	63±10.0
Length of last flying bout (min)	55±12.5	84±1.1	57±7.1
Length of other bouts (min)	34±9.5	98±25.4	80±31.3
Overall 100% MCP (ha)	42±59.4	127±120.5	231±114.2
Overall 85% core (ha)	16±7.5	30±6.9	22±8.7
% overall core of MCP	32±19.2	24±8.6	11±3.6
Nightly 100% MCP (ha)	32±14.6	107±69.0	87±43.6
Nightly 85% core (ha)	12±4.5	20±5.3	13±2.2
% nightly core of MCP	43±21.2	24±9.0	26±0.7
Overall maximum range from maternity roost (km)	1.2±0.5	1.8±0.4	2.9±0.9
Overall range span (km)	1.3±0.5	1.9±0.5	2.7±1.1
Nightly range span (km)	0.8±0.2	0.8±0.3	1.9±1.2
Distance travelled per night (km)	3.5±0.8	7.4±1.2	7.0±1.6

Table 3.2b. Summary of the flight data for *Rhinolophus hipposideros* within the high quality landscape. Sample sizes are provided in Table 3.1.

Variable	Late Pregnancy	Lactation	Post-Lactation
Emergence (min after sunset)	19±5.6	7±6.4	15±6.9
Final return to roost (min before sunrise)	19±3.5	16±10.2	22±1.5
Total night time from emergence to final return time (min)	412±3.5	466±5.4	565±11.7
Overall flying time (min)	200±67.2	286±31.5	334±39.5
% overall flying time of total night time	49±16.5	62±6.2	59±7.9
Number of flying bouts	3.7±2.0	4.9±0.4	4.4±0.5
Average length of flying bout (min)	62±22.2	59±6.5	79±5.7
Length of first flying bout (min)	69±42.6	59±8.6	105±20.3
Length of last flying bout (min)	58±50.3	85±34.6	73±5.0
Length of other bouts (min)	31±12.6	51±14.1	66±9.2
Overall 100% MCP (ha)	88±126.5	130±22.9	173±84.2
Overall 85% core (ha)	20±12.2	22±9.3	31±4.2
% overall core of MCP	18±9.6	17±4.7	20±6.3
Nightly 100% MCP (ha)	62±33.3	76±10.2	111±62.3
Nightly 85% core (ha)	15±6.7	15±6.9	18±1.6
% nightly core of MCP	30±16.4	22±11.3	19±6.7
Overall maximum range from maternity roost (km)	1.9±0.8	1.7±0.5	2.3±0.9
Overall range span (km)	2.0±0.7	2.0±0.3	2.3±0.9
Nightly range span (km)	1.3±0.5	1.7±0.2	2.2±1.0
Distance travelled per night (km)	3.9±2.2	6.5±2.0	7.8±0.5

Table 3.2c. Summary of the flight data for *Rhinolophus hipposideros* within the upland landscape. Sample sizes are provided in Table 3.1.

Variable	Lowland	High quality	Upland
Emergence (min after sunset)	31±11.8	30±13.3	14±7.9
Final return to roost (min before sunrise)	35±6.3	31±7.8	19±6.3
Total night time from emergence to final return time (min)	443±44.7	470±97.1	481±67.7
Overall flying time (min)	258±63.6	275±83.0	273±72.5
% overall flying time of total night time	59±14.9	58±10.7	56±11.4
Number of flying bouts	3.5±1.1	4.2±1.6	4.4±1.2
Mean length of flying bout (min)	85±35.0	70±22.2	67±15.0
Length of first flying bout (min)	102±54.0	67±23.0	77±31.9
Length of last flying bout (min)	63±36.0	64±15.8	72±32.8
Length of other bouts (min)	54±35.3	71±35.3	49±18.2
Overall 100% MCP (ha)	177±136.0	150±108.3	147±65.8
Overall 85% core (ha)	39±33.2	23±9.1	25±9.5
% overall core of MCP	25±13.9	22±14.2	18±6.4
Nightly 100% MCP (ha)	106±93.2	75±53.4	83±41.9
Nightly 85% core (ha)	24±14.9	15±5.4	16±5.0
% nightly core of MCP	32±15.5	31±14.6	23±11.7
Overall maximum range from maternity roost (km)	2.0±1.1	2.0±0.9	2.0±0.7
Overall range span (km)	2.2±1.1	2.0±0.9	2.1±0.6
Nightly range span (km)	1.7±1.0	1.5±0.5	1.7±0.7
Distance travelled per night (km)	6.3±2.9	6.0±2.1	6.1±2.3

Table 3.3. Summary of the flight data for adult *Rhinolophus hipposideros* within three different landscape types in Britain. Data are pooled for each site throughout the breeding season.

Return time

Time of return to roost differed significantly between localities (GLM, $F_{2,45}$ = 14.49, $p < 0.001$) but not according to breeding status (GLM, $F_{5,45} = 1.26$, NS). Multiple comparisons for locality indicate that the mean return time at the lowland and high quality landscapes were not significantly different (at 35 and 31 min before sunrise respectively) but that the return time at the upland site was significantly later (at 19 min before sunrise) compared with the other sites. There was a significant effect of cloud cover (GLM, $F_{1,45} = 5.49$, $p < 0.05$) on return time. The coefficient was negative so increased cloud cover resulted in the bats returning to the roost later. Any interaction terms and temperature were removed during model simplification.

Total flying time

The bats spent mean range of 258-275 min of the night flying, which comprised 56-59 % of the total night time. Total flying time did not differ among landscape types (GLM, $F_{2,43} = 0.22$, NS) but was affected by breeding status (GLM, $F_{5,43}$ = 4.64, $p < 0.01$) with lactating females and juvenile bats flying the longest. Multiple comparisons for status indicated the only significant differences were that lactating females flew for significantly longer than females during early and late pregnancy and that juveniles flew longer than bats in late pregnancy. Total flying time was significantly affected by minimum temperature (GLM, $F_{1,43} = 13.63$, $p <$ 0.01). The coefficient was negative so warmer temperatures reflected short flying times. Total flying time was also significantly affected by average rainfall (inverse transformed) (GLM, $F_{1,43} = 5.70$, $p < 0.05$) and average wind speed (GLM, $F_{1,43}$ = 5.70, $p < 0.01$). The coefficients were both were positive so stronger winds or increased rainfall reflected longer flying times. All interaction terms were removed during model simplification.

As night time varies according to season, the proportion of the night time spent flying (arcsine transformed) was investigated and was also found not to vary among landscapes (GLM, $F_{2,38} = 2.04$, NS) but did vary according to breeding

status (GLM, $F_{5,38} = 4.90$, $p < 0.01$). Multiple comparisons for status indicated that adult females during early pregnancy and post-lactation and nulliparous females spent a significantly smaller proportion of the night flying than lactating females. The covariates were all significant: minimum temperature (GLM, $F_{1,38} = 6.62$, $p < 0.05$), average rainfall (GLM, $F_{1,38} = 6.99$, $p < 0.05$) and average wind speed (GLM, $F_{1,38} = 5.14$, $p < 0.05$). The coefficients indicated that warmer temperatures reflected a smaller proportion of night time spent flying whereas stronger winds or increased rainfall reflected a greater proportion of night time spent flying. In addition there was a significant interaction between status and average wind speed, indicating that wind speed affected proportion of time spent flying in different ways at different stages of the breeding cycle. Females in late pregnancy and lactation and juveniles decreased the proportion of the night time spent flying during windier conditions whereas the opposite occurred in adult females in early pregnancy and, post-lactation and nulliparous females.

Flying bouts

The bats showed multimodal phases of activity with one to nine flying bouts (mean range 2.6-5.5 depending on locality and breeding status). One foraging bout per night was rare, occurring in just five of the 145 nights with full data. The number of flying bouts did not varying between landscapes (GLM, $F_{2,45} = 1.68$, NS) but was affected by breeding status (GLM, $F_{5,45} = 2.89$, $p < 0.01$). Multiple comparisons for status indicated that number of foraging bouts was significantly smaller in early and late pregnancy compared with post-lactation. Average wind speed significantly affected number of bouts (GLM, $F_{1,45} = 5.23$, $p < 0.05$) with stronger winds associated with more bouts. Minimum temperature, average rainfall and all interaction terms were removed during model simplification.

In general the first flying bout was the longest of the night (mean range 59-128 min) followed by the last bout before sunrise (mean range 47-88 min for females, mean 100 min for juveniles in the lowland landscape). One-way ANOVA showed there was significant difference between the length of bouts (GLM, $F_{2,159} = 8.74$, $p < 0.001$). Post hoc Tukey's pairwise comparisons revealed the first flying bout

was significantly longer than both the final and all in-between bouts combined (which were not significantly different from one another).

Length of the first flying bout (log transformed) varied between landscapes (GLM, $F_{2,33} = 4.31$, $p < 0.05$) but was not affected by breeding status (GLM, $F_{5,33} = 1.909$, NS). Multiple comparisons indicated that the length of the first flying bout was significantly longer in the lowland landscape. There were significant interactions between breeding status and minimum temperature and average wind speed (GLM, $F_{5,33} = 2.74$, $p < 0.05$; $F_{5,33} = 4.89$, $p < 0.01$) implying that environmental conditions affected length of first flying bout in different ways at different stages of the breeding cycle.

Length of the average flying bout (square root transformed) did not vary between landscapes (GLM, $F_{2,38} = 1.49$, NS) and was not affected by breeding status (GLM, $F_{5,38} = 1.50$, NS), minimum air temperature (GLM, $F_{1,38} = 2.44$, NS) or rainfall (inverse transformed) (GLM, $F_{1,38} = 0.08$, NS). There were significant interactions between breeding status and average wind speed (GLM, $F_{5,38} = 2.73$, $p < 0.05$) with adult females being negatively affected in late pregnancy, lactation and post-lactation. Other interaction terms were removed during model simplification.

Ranging behaviour

There were differences in home range according to breeding status but the overall mean 100 % MCP for adult females in the high quality and upland landscapes were similar (150 ha, range 21-282 ha, and 147 ha, range 43-269 ha, respectively), whereas it was 177 ha (range 9-517 ha) in the lowland landscape. The same pattern was observed for the nightly 100 % MCP and overall and nightly 85 % cores.

The largest mean in overall home ranges was recorded in juveniles at the lowland site (mean 261 ha, range 25-394 ha). In 5 of the 6 juveniles radio-tracked I observed a general trend of increasing home range size with time. Early flights were characterised by their limited range and short duration, with home ranges for

3 individuals not reaching asymptotes by the end of the tracking session (Figure 3.1).

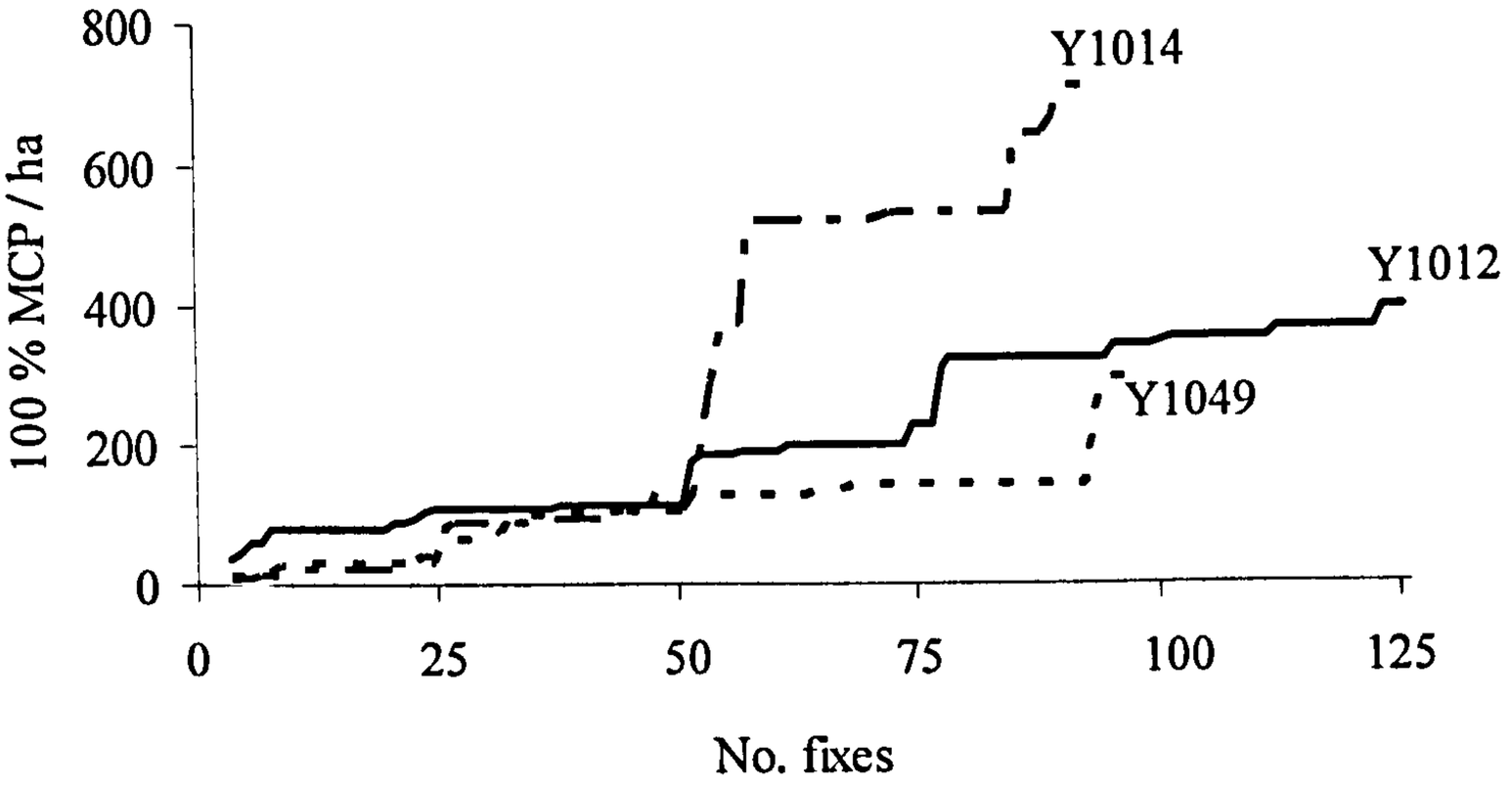

Figure 3.1. Plots of increasing home range (based on 100 % minimum convex polygon (MCP)) *vs.* number of fixes for three juvenile *Rhinolophus hipposideros* radio-tracked in the lowland landscape. Plots do not reach asymptotes despite at least 95 fixes being collected per individual. Y1012 and Y1049 (both male) were radio-tagged in mid-August. Y1014 (female) was tagged in mid-September.

Statistically the overall 100 % MCP (square root transformed) and overall 85 % core (log transformed) did not vary between landscapes (GLM, $F_{2,46} = 0.02$, NS; $F_{2,46} = 0.15$, NS) and was not affected by breeding status (GLM, $F_{5,46} = 0.62$, NS; $F_{5,46} = 0.65$, NS). Minimum temperature and average rainfall were removed during model simplification. Similarly the nightly 100 % MCP (log transformed) and nightly 85% core did not vary between landscapes (GLM, $F_{2,46} = 0.14$, NS; $F_{2,46} = 0.30$, NS) and were not affected by breeding status (GLM, $F_{5,46} = 0.78$, NS; $F_{5,46} = 0.49$, NS). Minimum air temperature, average rainfall, wind speed and interaction terms were removed during model simplification.

The mean maximum range distance from the maternity roost for adult females was identical in each landscape (2.0 km) although the maximum distance an individual adult female was recorded flying to did vary. The value was 4.1 km for lowland, 3.5 km for high quality and 3.3 km for upland. Nulliparous females and juveniles

were recorded a maximum of 4.5 km and 3.8 km respectively from the maternity roost in the lowland landscape.

The overall mean range span was very similar among landscape types (2.0-2.2 km) and between reproductive classes in the lowland and upland landscapes, with a pattern of increasing range span observed in the high quality landscape. Overall mean range span (square root transformed) and mean nightly range span did not vary between landscapes (GLM, $F_{2,46} = 0.06$, NS; $F_{2,46} = 0.18$, NS) and were not affected by breeding status (GLM, $F_{5,46} = 0.36$, NS; $F_{5,46} = 0.70$, NS). Minimum temperature, average wind speed, average rainfall and interaction terms were removed during model simplification.

The overall mean maximum distance travelled per night was broadly consistent for adult females within the three landscapes (6.0-6.3 km) although this parameter did vary through the breeding season, with smallest distances recorded in late pregnancy, particularly in the high quality and upland localities. Statistically however the mean total distance travelled per night (square root transformed) did not vary according to locality (GLM, $F_{2,45} = 0.44$, NS) or breeding status (GLM, $F_{5,46} = 0.19$, $p = 0.07$). However minimum air temperature did have an effect (GLM, $F_{1,46} = 4.71$, $p < 0.05$). The coefficient was negative so colder temperatures reflected greater distances travelled. Average rainfall, average wind speed and interaction terms were removed during model simplification.

Overlap between individual ranges

Overlap of home ranges was broadly similar in the lowland and upland landscapes, where home ranges overlapped by 18-43 % and 15-57 % respectively for 100 % MCPs and by 5-33 % and 9-34 % respectively in 85 % core areas, although differences are evident between reproductive classes. In the high quality landscape, overlap for 100 % MCPs was also similar (16-39 %) but overlap was considerably less in 85 % core areas (0-5 %) (Table 3.4).

Overlap comparison	Lowland		High quality		Upland	
	100% MCP	85% core	100% MCP	85% core	100% MCP	85% core
Adult female						
Early pregnancy	36.4±26.9	7.2±6.6				
Late pregnancy	27.7±16.1	22.6±15.1	15.5±15.9	2.8±2.4	14.7±5.6	9.1±5.2
Lactation	38.0±24.2	28.8±10.9	38.7±18.1	0±0	32.4±17.0	34.0±15.9
Post-lactation	29.7±24.2	7.1±7.4	30.7±13.2	4.6±4.7	57.2±23.6	34.0±7.4
Nulliparous female	17.5±15.3	4.8±3.6				
Juvenile	43.4±30.9	32.5±21.2				

Table 3.4. Percentage home-range overlap (of 100% minimum convex polygons (MCP) and 85% core areas) for *Rhinolophus hipposideros* radio-tracked in three different landscapes. Indices of overlap are means ±1 SD. Sample sizes are provided in Table 3.1.

As survey work was most comprehensive at the lowland roost I have also considered the overlap between all radio-tracked individuals regardless of reproductive status. Home ranges overlapped by mean 32.1 % ± 17.9 (range 3.3-70.1 %) for 100 % MCPs and by mean 16.9 ± 9.8 (range 0-33.6 %) in 85 % core areas. Overlap of core home ranges was therefore greater than average during late pregnancy and lactation and for juveniles.

Indices of percentage home-range overlap of 100 % MCPs did not vary significantly among localities (GLM, $F_{2,46} = 0.19$, NS) and reproductive classes (GLM, $F_{5,46} = 1.89$, NS). However indices of 85 % cores did vary significantly among localities (GLM, $F_{2,46} = 8.41$, $p < 0.01$) and according to breeding status (GLM, $F_{5,46} = 4.63$, $p < 0.01$). Multiple comparisons for locality indicate that the overlap indices within the lowland and upland landscapes were not significantly different but that the degree of overlap of core home ranges within the high quality landscape was significantly lower. Multiple comparisons for breeding status indicated that core home ranges of juveniles overlapped significantly more than those of females in early pregnancy and that both lactating females and juveniles showed greater overlap than nulliparous females.

Estimation of foraging density

Within the lowland landscape 50 % of all of the radio-tracking fixes were within 0.5 km of the maternity roost. Using fixes for adult females only gave a figure of 0.6 km. Within the high quality and upland landscapes the figure was 1.1 km and 0.9 km respectively. Assuming a random sample of bats, this implies that bats from the colonies forage half of their time within these distances of the roosts. Given that the mean maximum distance was consistent between landscapes it allows a comparison of estimated density of bats in each locality. Approximately 200 bats occur within the lowland colony (including juveniles), so within 2.0 km the estimated density of foraging bats was 0.13 bats/ha using all fixes. Colony size for high quality and upland landscapes are *c.* 750 and *c.* 130 respectively, giving an estimated density of 0.50 bats/ha and 0.09 bats/ha at 2.0 km. The variation in estimated density of bats around the three maternity roosts is given in Figure 3.2.

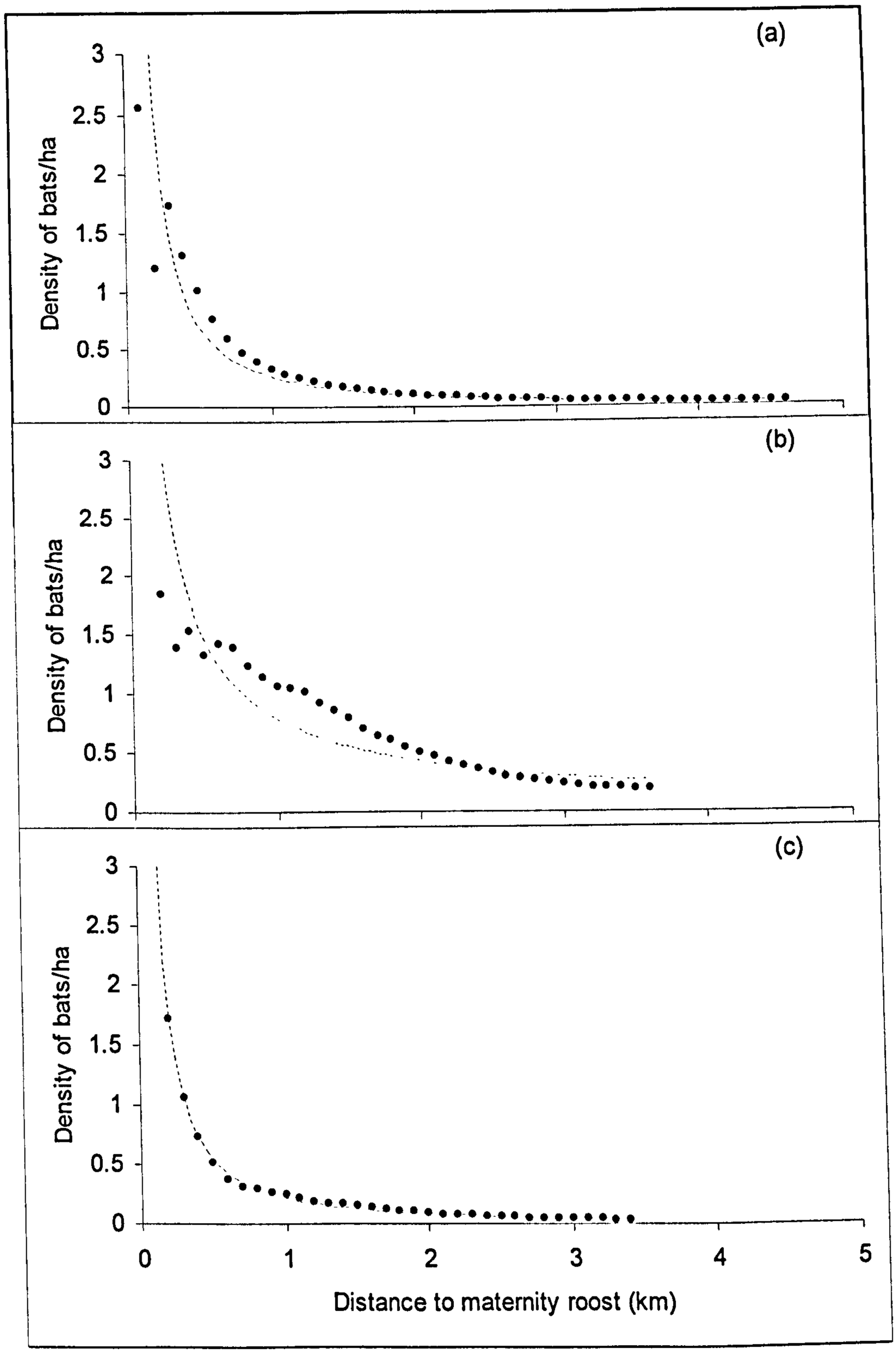

Figure 3.2. Variation in the estimated density of *Rhinolophus hipposideros* with distance from the maternity roost in three different landscape types: lowland (a), high quality (b) and upland (c). Dashed line = power trendline. The density of bats has been calculated using the utilisation density of radio-tracking fixes within successive zones (100 m, 200 m, 300 m, ...) around the maternity roost.

Potential barriers to commuting

The utilisation distributions calculated previously indicated that fixes were not uniform around the maternity roost, with 50 % of fixes occurring, for example, 0.5 km from the lowland roost. At the lowland locality the maternity roost is directly adjacent to a main single carriageway A-road. The vicinity of the roost is dissected by two A-roads (Figure 3.3), together with numerous smaller roads. 47 % of the home ranges of the bats sampled span two roads and 36 % span one road with only 17 % of the home ranges containing no main roads, suggesting that roads are not creating a barrier to dispersal.

The main roads divide the maximum range circle (MRC) (centred on the roost) into four sections (Figure 3.3). The fixes were not uniformly distributed within these sections (circular statistics, $\chi^2 = 858.7$, d.f. = 3, $p < 0.001$). Although the section south of and containing the roost (section A) and involving no road crossings was used more than expected, the section north of the roost (section C) involving two road crossings was used as expected. This further implies that the roads are not restricting movement. However this analysis does not take into account the effect of habitat preferences, which will be explored in Chapter 5.

Only one main road (single carriageway) exists within the colony MRC in the high quality landscape. It largely follows the course of the main River Wye, which could also potentially be a barrier to movement, given its large width (40-45 m) and lack of continuous bank side tree cover. 4 of the home ranges of the bats sampled spanned the River Wye and road but only one bat (a pregnant female) was actually recorded crossing these features. No direct observations were made but the bat emerged from the roost and commuted directly west over the river and road to its core area. Only a small proportion of this colony was sampled (*c.* 1 %) so it is likely that rather than being the exception other bats from the colony would also cross these features.

In the upland landscape all roads within the colony MRC are narrow lanes and no main rivers exist. However analysis of habitat use suggests bats are avoiding the open moorland (heathland / continuous bracken), both in the upland landscape and

in the lowland area where heathland / continuous bracken exists. This habitat may be either a barrier to commuting and / or be of poor quality for foraging and this will be explored further in Chapter 5.

General observations

On 148 occasions active (excluding commuting) bats were tracked to within ±10 m. The majority of these fixes (over 95 %) were associated with tree cover, of variable structure and species. *R. hipposideros* were recorded showing presumed foraging behaviour within solitary standard trees and standards within managed hedgerows, within groups of trees (ranging from a few trees to extensive woodland), within tall scrub and unmanaged hedges (greater than 3 m in height with a continuous or semi-continuous canopy structure), and were recorded using the full height of the tree canopy structure. A range of tree species were noted: ash *Fraxinus excelsior,* oak *Quercus* spp., sycamore *Acer pseudoplatanus,* hazel *Corylus avellana*, alder *Alnus glutinosa*, small-leaved lime *Tilia cordata,* elm *Ulmus* spp., willow *Salix* spp., horse-chestnut *Aesculus hippocastanum,* yew *Taxus baccata.* Despite being so close to the subject bats were rarely detected on an ultrasound detector and rarely seen suggesting they were flying within or close to the canopy. Bats were also recorded flying around trees of variable age. For example, during early pregnancy in May two bats were observed flying in the canopy of young and semi-mature trees as opposed to the adjacent mature trees. It was observed that the mature trees were still in bud whilst the younger trees were already in leaf.

Bats were also occasionally recorded in presumed foraging behaviour over open areas, above pasture fields and above the headlands of arable fields but there were no direct sightings so it is not possible to comment on height of flight. However the bats were moving around consistently, rather than remaining in one small area.

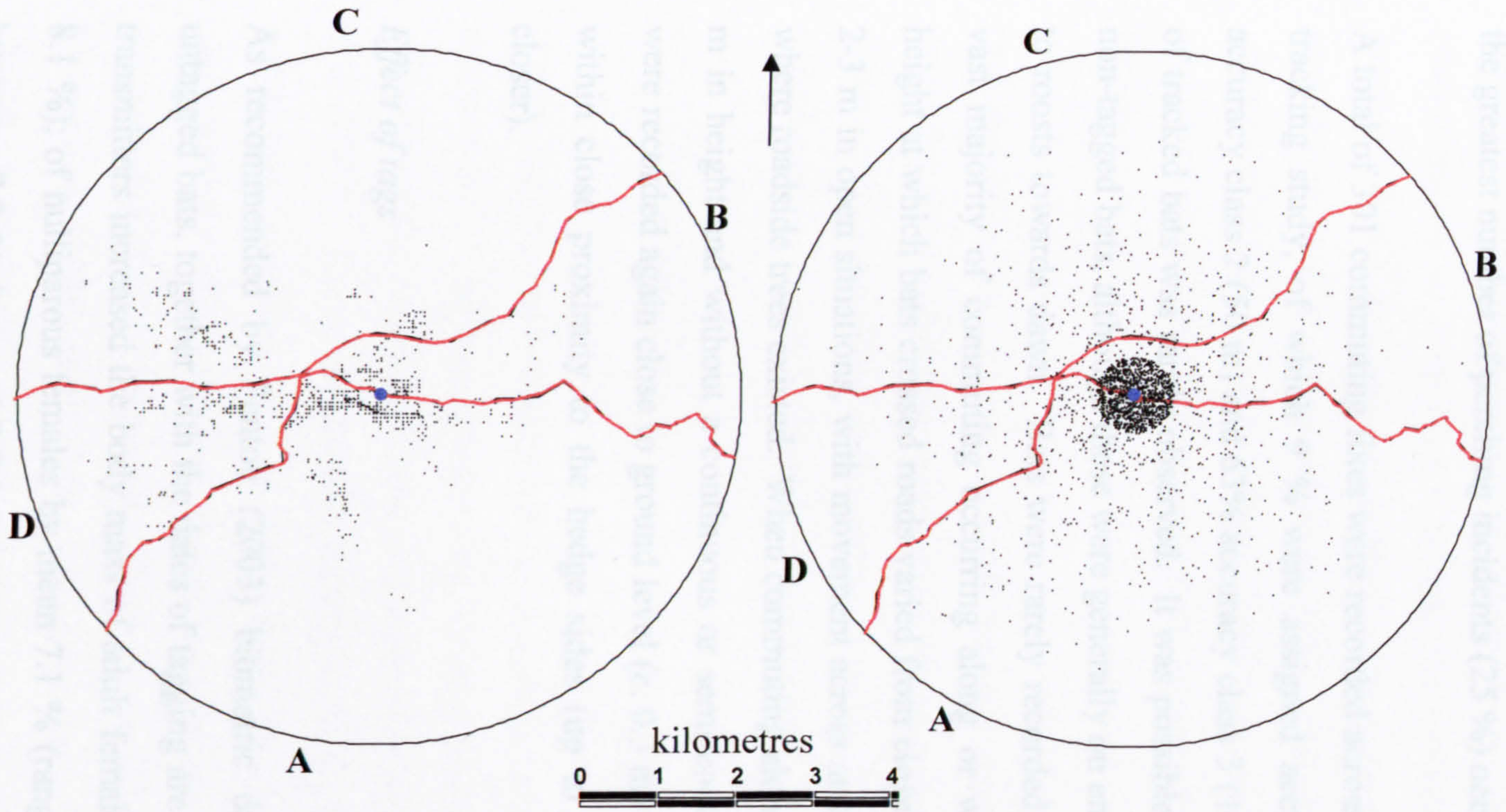

Figure 3.3. The maximum range circle (MRC), centred on the lowland landscape maternity roost (●) and the course of two main single carriageway A-roads (—), which dissect the MRC into four sections A-D. *Left* - The distribution of the 2124 fixes recorded during the radio-tracking of *Rhinolophus hipposideros*. *Right* – Random fixes generated using the utilisation distribution. The MRC was sub-divided into concentric rings of 0.5 km radii and random fixes (2124 in total) were generated using a uniform distribution within each ring. 50 % of fixes occur within 0.5 km of the roost. Sections A and D were used more than expected from the model distribution. Section B was used less than expected and Section C (involving two road crossings) was used as expected.

A total of 117 fixes (at all resolutions) were associated with perching behaviour and it was assumed that bats were either resting briefly or fly-catching, although there were no direct observations of this. There appeared to be no clear pattern with perching behaviour according to reproductive status among localities but overall it appeared more common during late pregnancy and lactation. For example in the high quality landscape 60 % of fixes associated with perching behaviour were recorded during late pregnancy whereas in the lowland landscape the greatest number of perching incidents (25 %) occurred during lactation.

A total of 301 commuting fixes were recorded across the three localities during the tracking study, of which 9 % were assigned accuracy class 1 (10 m), 28 % accuracy class 2 (50 m) and 63% accuracy class 3 (100 m). Commuting behaviour of tracked bats was rarely observed. It was possible to also make observations on non-tagged bats, although these were generally on emergence at dusk and on return to roosts towards dawn. Bats were rarely recorded crossing open fields with the vast majority of commuting occurring along or within vegetation cover. The height at which bats crossed roads varied from close to ground level (*c.* 0.15 m) to 2-3 m in open situations, with movement across at canopy level in some instances where roadside trees existed. When commuting along managed hedges (less than 3 m in height and without a continuous or semi-continuous canopy structure) bats were recorded again close to ground level (*c.* 0.3 m) up to hedge height but usually within close proximity to the hedge sides (up to *c.* 1.0-1.5 m away, typically closer).

Effect of tags

As recommended by Fenton (2003) biometric data collected on tagged and untagged bats, together with the dates of tagging are provided in Appendix 1. The transmitters increased the body mass of adult females by mean 6.2 % (range 4.9-8.1 %); of nulliparous females by mean 7.1 % (range 6.5-8.8 %) and of juveniles by mean 7.2 % (range 6.7-7.8 %). The increased body mass recorded in adult females is comparable with the 4.5-8.1 % increase documented by Bontadina *et al.* (2002) in their study on *R. hipposideros*. The authors analysed in detail the

potential effects of tags and concluded the transmitters had no demonstrable adverse effect on flight behaviour.

In this study 14 individuals were subsequently re-caught after tagging either in the same year or following years. This enabled a direct evaluation of physical changes as advocated by Withey *et al.* (2001). The area between the scapulae where the transmitters were attached was checked. There were no skin abrasions evident and the fur had either re-grown back completely or the short under-fur was present (depending on duration after tagging). The forearm/wing was also checked for damage. Two individuals had minor ring damage, described as 'wing discoloured around ring' and 'some blistering on wing'. Bats had evidently bred successfully subsequent to tagging. For example, Y1019, an adult female was tagged in the late pregnancy period and was re-caught in August of the same year when she was lactating.

One exception was Y1036, an adult female tagged during post-lactation. Nine days after tagging the transmitter signal became consistently steady. The bat was subsequently found dead in the maternity roost. The antenna of the tag was found to be caught in a crack in the ridge beam timber.

3.5 *Discussion*

In this study the radio-transmitters used were mean 6.2-7.2 % of body mass, which is above the 5% as recommended by Aldridge and Brigham (1988) although they were within the American Society of Mammalosist's guideline of 5-10% (Gannon et al. 2007). Kurta and Murray (2002) radio tracked 11 female *Myotis sodalis* using tags weighing 8% of body mass (*c.* 7g) and found that all were reproductively active and had normal body masses over three subsequent years, suggesting negligible long-term effects of the radio tracking process. However Rayner *et al.* (1989) caution that a load of between 5 and 10% of mass represents a change in mechanical flight power of between 8 and 15%, which becomes significant since total flight energy may comprise as much as one-quarter or one-third of daily energy expenditure. The energy required to transport loads can only be obtained by inceasing total foraging intake or by diverting energy from other

sources. Therefore, time budet and other behavioural data obtained by radio-tracking may overestimate time normally spent in flight or foraging, and may distort the type of foraging adopted (Rayner et al. 1989). Aldridge and Brigham (1988) demonstrated that increases in body mass of 5 to 33% in female *Myotis yumanensis* resulted in reduced maneuverability. *R. hipposideros* is a highly manoeuvrable species (Norberg and Rayner 1987) and Aldridge and Rautenbach (1987) found that such bats were characterised by the ability to forage in cluttered environments. Therefore a decrease in maneuverability would be expected to result in foraging in less cluttered situations. However the behaviour of tagged bats in this study was generally similar to observations of *R. hipposideros* reported previously through field observations of wild free-flying bats (McAney and Fairley 1988b, Jones and Rayner 1989).

The behaviour of commuting bats in this study was also generally similar to observations of *R. hipposideros* reported by Schofield (1996), Schofield *et al.* (2002) and Cresswell Associates (2004). Bats were rarely recorded crossing open fields with the vast majority of commuting occurring close to or within vegetation cover, for example hedgerows, woodland and gardens. This may make them vulnerable to fragmentation of habitats. Bats were often observed crossing roads and an assessment of dispersal in relation to the main roads surrounding lowland roost implied that the roads were not restricting movement.

The observed behaviour patterns may reflect their foraging strategy, predator-avoidance strategy, and distribution of prey items. In the majority of close encounters in this study the bats were flying within or close to a tree canopy. The use of canopy structures agrees with predictions gained from their flight morphology and echolocation (Aldridge and Rautenbach 1987, Jones and Rayner 1989) whilst the use of open habitats is more unexpected. Non-migrating insects occur at high concentrations around the crown, and in the lee, of vegetation and shelter belts and densities decrease away from such structures and are distributed nearer the ground (Lewis 1969, 1970). For example, Downs and Racey (2006) found that insects were present in higher densities alongside treelines than in open spaces approximately 35 m away. It is likely therefore that in such situations *R. hipposideros* forage close to the ground and Jones and Rayner (1989) reported that

bats were observed gleaning prey off the ground. Fly-catching was not observed by these authors but Schofield (1996) observed female *R. hipposideros* fly-catching during late pregnancy, suggesting that it is a viable foraging strategy when the bats' wing-loading is high. Perching in trees, which may be associated with fly-catching, was recorded in adult females throughout the breeding season but particularly in late pregnancy and lactation, together with nulliparous females and juveniles in this study. Schofield *et al.* (2002) also recorded perch hunting behaviour in their radio-tracking study.

As detailed in the Introduction, a number of radio-tracking studies of *R. hipposideros* have previously been undertaken (refer to Table 1.1, Chapter 1). Of particular interest is the study by Bontadina *et al.* (2002) who radio-tracked *R. hipposideros* from a 300-strong maternity roost in the Lower Wye Valley *c.* 8.4 km from the high quality roost used in the current study. The range parameters for 5 adult females radio-tracked in July and August were substantially lower than those recorded in this study, although the authors state that the home range of several individuals included had not reached asymptotes so should be regarded as minimum values. In contrast the range parameters for 5 adult females tracked in August and September by Cresswell Associates (2004) in Gloucestershire, a landscape most comparable with the lowland landscape type used in my study, were larger, although one individual had a home range of 1155 ha which was exceptional. Removing the data from this bat gives an average of 194 ha, a value similar to mine. The range parameters recorded by Schofield *et al.* (2002) for pregnant and lactating females in Radnor, Wales, were broadly similar whilst the values for post-lactation were somewhat reduced. In a study undertaken outside Britain, Holzhaider *et al.* (2002) found the tracked bat spending a mean 60.4% of the night active, which is once again comparable with my findings.

Within my study the behaviour of *R. hipposideros* was in general remarkably consistent within the three contrasting landscapes, despite the high quality roost supporting over 4 times as many bats as the lowland and upland roosts. It has been postulated that large colony size increases the foraging range of individuals (Jones et al. 1995), but my study clearly indicates that this is not the case for the three roosts considered. Although the maximum distance an individual adult female was

recorded did vary, mean overall foraging range was identical, with range span, distance travelled per night, proportion of night time spent flying, average length of flying bout and number of flying bouts all very similar. In addition although differences were observed in home ranges and core areas, with figures smaller in the high quality and upland landscapes, these were not significant.

The similarity of many of the range parameters suggests that rather than adapting their behaviour to the landscape and/or colony size *R. hipposideros* largely adopt the same behaviour regardless of their surroundings. Morphologically the species has a low aspect ratio of 5.7, low wing loading of 5.1 N m^{-2} and relatively low flight speed (Norberg and Rayner 1987, Neuweiler 1989, Jones and Rydell 1994). Bats with lower aspect ratios tend not to travel as far as species with higher aspect ratios due to increased drag on the wings reducing aerodynamic efficiency, and Jones *et al.* (1995) predicted the foraging range of *R. hipposideros* to be 1.3 km based on their morphology. Although this figure is less than the 2.0 km recorded here, the consistency of range parameters within the three contrasting landscapes in this study does suggest that perhaps there is an optimal behaviour that is constrained by the species' morphology, which the bats are adopting regardless of the surrounding landscape.

Pipistrellus sp. are a similar size to *R. hipposideros* with a slightly higher wing loading but they have a much higher aspect ratio, resulting in increased aerodynamic efficiency and the ability to fly further. The commuting costs of *Pipistrellus* sp. roosting 2 km from suitable foraging habitats were less than 2.5 % of the daily energy budget and commuting costs became prohibitive only when foraging areas were more than 5 km distant (Speakman et al. 1991). A similar trend may be happening with *R. hipposideros*, perhaps with commuting costs for the colony as a whole becoming prohibitive beyond 2 km from the maternity roost, and this warrants further study.

Jones and Rydell (1994) found that emergence time appears to be a function of dietary specializations and foraging strategy, with slow flying species, such as *R. hipposideros*, emerging later. The authors recorded *R. hipposideros* first emerging 19 min after sunset with a median emergence of 30 min, whilst McAney and

Fairley (1988a) recorded a mean emergence time of 29-33 min. Emergence time was found to vary among the landscape types, with bats in the upland landscape emerging significantly earlier than those in the lowland and high quality landscapes, which both emerged at similar times to previous studies (31 and 30 min respectively).

Numerous studies have shown that emergence time is dependent upon a range of factors. For example, tree cover near roosts results in earlier emergence times (Jones et al. 1995, Jenkins et al. 1998, Duvergé et al. 2000) whereas the application of external white light at roost entrances reduces emergence (Downs et al. 2003). Schofield (1996) showed a strong positive correlation between the median emergence time of *R. hipposideros* and the time at which light levels fell to 10 lux and between the median return time and the time at which light levels reached 10 lux. Although cloud cover did not affect emergence in my study I did find that increased cloud cover resulted in the bats returning to the roost later. The exit from the lowland roost was adjacent to a main road and was subject to regular external lighting from passing traffic during which time bats temporarily failed to emerge or 'light sample' (brief emergence/return (DeCoursey and DeCoursey 1964)) (pers. obs.). In contrast the high quality and upland roost exits were directly adjacent to woodland cover, which suggests the bats may have been able to emerge earlier without increasing predation risk.

Swift (1980) showed a strong linear relationship between average rates of emergence and colony size in *Pipistrellus* sp., and Avery (1986) found the time of emergence of the first bat strongly dependent on colony size. This would explain why bats in the high quality roost emerged later than the upland roost, despite similarity of exit point characteristics and adjacent tree cover, as over five times the number of bats are present. In Chapter 2 I described how Trichoptera, which are usually on the wing at dusk (Chinery 1993), was most abundant in the diet composition within the upland landscape. By emerging earlier than previously recorded in other studies, *R. hipposideros* in this landscape may have been able to begin foraging before the abundance of Trichoptera declined as the night progressed.

Emergence time also varied according to breeding status although this was not significant, whereas McAney and Fairley (1988a) did find significant difference in emergence time between sexes and reproductive classes. In my study lactating females emerged earlier than bats in late pregnancy and during post-lactation in all three landscape types which supports the findings of previous studies (Duvergé et al. 2000, Reiter 2002). This may be due to the higher energy demands during lactation (Racey and Speakman 1987).

This higher energy requirement is also reflected in changes to amount of night time spent flying, and lactating *R. hipposideros* flew for significantly longer than females during early and late pregnancy. Whilst time budget data obtained by radio-tracking may overestimate time normally spent in flight or foraging (Rayner et al. 1989) several studies involving field observations of free-flying bats rather than radio-tracking have shown flight durations increase during lactation (Rydell 1993, Bartonička and Řehák 2004) which support an increase in food consumption then. Rydell (1993) suggested that, at high latitudes, insectivorous bats may act as energy maximisers, and forage opportunistically when conditions permit, rather than as time minimisers, whereby foraging time reflects energy demands and would increase slowly during pregnancy and then quickly as lactation advanced. The latter hypothesis conforms with the behaviour observed in *R. hipposideros*.

Range size, as well as foraging times, could be expected to be greater in bats with higher energy demands. However the various home range size parameters of *R. hipposideros* did not vary significantly according to reproductive status. The largest home ranges (based on 100 % MCP) occurred for juveniles in the lowland landscape and during post-lactation for adult females within the high quality and upland landscapes. Juveniles have a high energy requirement and post-natal growth is one of the fastest recorded for any bat species (Schofield 1996) which could explain their large home range size. In 5 of the 6 juveniles radio-tracked I observed a general trend of increasing home range size with time, with early flights characterised by their short duration and limited range, and with home ranges for 3 individuals not reaching asymptotes by the end of the tracking session. Similar behaviour has been recorded in *Rhinolophus ferrumequinum* (Jones et al. 1995), *P. pipistrellus* (Racey and Swift 1985) and in *Myotis myotis* (Audet 1990). As

previously discussed, home range size could be expected to be highest in lactating females rather than during post-lactation. A similar expansion of home ranges was found in *Chalinolobus tuberculatus* by O'Donnell (2001). This coincided with juveniles beginning to fly and it was thought that movement by adults to more distant foraging areas would potentially reduce competition with juveniles. An alternative explanation is that this increase may reflect the onset of mating in September (Schofield 1996). In *Rhinolophus* spp. solitary males occupy territories for a period of days/weeks during which time females visit and select a male for mating (Ransome 1990). Therefore females may be travelling to mating sites outside of their normal foraging range and evidence for this was shown by some individuals being recorded visiting a night roost outside of their normal core area on one occasion only during the tracking session (pers. obs).

Despite this expansion of home range during post-lactation, within the lowland landscape overlap of core home ranges was actually less than average at this time. Interestingly overlap indices were greater than average during late pregnancy and lactation and for juveniles, when energetic demands are greatest. Overlap indices within the lowland and upland landscapes where density of bats are estimated to be 0.13 and 0.09 bats/ha respectively were similar and significantly higher than the high quality landscape (estimated density 0.5 bats/ha). Following O'Donnell (2001) home ranges with low overlap provide a mechanism for spacing bats in the landscape to minimise potential competition for food resources and forcing increased overlap between individuals would reduce fitness. However comparisons between overlaps should be regarded with caution due to small sample sizes in the high quality and upland landscapes with less than 10% of the colony being radio-tracked. In *R. ferrumequinum* relatedness levels among females correlated positively with home range overlap and matrilineal kin shared feeding grounds to a greater extent than non-kin (Rossiter et al. 2002). There fore it is possible that due to small sample sizes closely related females were not included in the sample and overlap estimates may be inaccurate.

The activity of *R. hipposideros* was affected by weather conditions in various ways. Colder temperatures reflected a greater proportion of the night time spent flying and greater distances travelled during the night. In contrast Gaisler (1963c)

found no direct evidence of the influence of temperature on the foraging activity of *R. hipposideros* whilst *R. ferrumequinum* was found to increase foraging activity with increasing temperatures (Duvergé 1996). In general activity of foraging bats is thought to be positively correlated with ambient temperature (Catto et al. 1995, Walsh and Harris 1996b, Vaughan et al. 1997, Gaisler et al. 1998, Erickson and West 2002). I also found increased rainfall resulted in a greater proportion of the night time spent flying. *R. hipposideros* were observed flying, and presumed foraging, in rainy conditions from drizzle to even heavy rainfall conditions, though more usually heavy rainfall did curtail activity temporarily with the individual returning to a night roost or perching in a tree. Holzhaider *et* al. (2002) also recorded *R. hipposideros* foraging during heavy rain. These relationships imply that colder temperatures and increasing rainfall affected quality of foraging resulting in bats needing to forage for longer than usual. This suggests that bats may aim to reach a target of energy consumption, and reaching this target takes longer in poorer conditions.

The effect of wind speed on activity parameters was not as clear cut as that of temperature and rainfall. In general stronger wind speed resulted in a greater proportion of the night time spent flying and a greater number of flying bouts. This may relate to the above theory of target energy consumption as wind speed has been found to negatively affect the abundance of dusk- and night-flying families of Diptera (such as Anisopodidae and Tipulidae) (Peng et al. 1992a) although Lewis (1969) found that insects accumulated near hedges more in windy weather. Interestingly my study indicated that the effects of wind speed varied at different stages of the breeding cycle. Females in early pregnancy and post lactation, together with nulliparous females spent a greater proportion of the night flying during windier conditions. In contrast females in late pregnancy and lactation and juveniles spent less time flying in windier conditions.

As detailed earlier, energetic costs are higher during lactation and for juvenile bats. Studies on *Plecotus auritus* strongly indicated that lactating bats were using compensating mechanisms in their energy budgets, possibly by a reduction in grooming activity (Speakman and Racey 1987, McLean and Speakman 1999). Daily torpor is a key component in the survival strategy of temperate bats

(Altringham 2003). Wilde *et al.* (1995) found that milk production was reduced while *Pipistrellus* sp. bats were torpid but that the response of the mammary glands to suckling was acute. Swift (1998) argues therefore that this acute response probably causes rapid milk production during the next bout of foraging away from the youngster so daily torpor could be utilized in lactation as compensation. However a study by Dietz and Kalko (2006) found that although female *M. daubentonii* did reduce their skin temperature to up to 6 °C below active temperature during lactation they avoided deep daily torpor. Similarly lactating *Eptesicus fuscus* use torpor rarely (Grinevitch et al. 1995). Therefore the difference in the effect of wind speed at different stages of the breeding cycle demonstrated by this study may suggest that *R. hipposideros* use compensation, possibly by a reduction in grooming activity as opposed to use of deep torpor, to offset reduced quality of foraging during periods with highest energetic costs and this warrants further study.

In Chapter 2 I suggested that gleaning is unlikely to be the principal foraging strategy for *R. hipposideros* with the majority of prey caught on the wing during aerial hawking. I futher suggested that feeding on swarming insects at dusk and dawn could play an important part in foraging based on the faecal composition and the nightly activity patterns of key prey items. The radio-tracking study gives further evidence to support this theory. Dietary studies of *Plecotus auritus* have shown that more than 40% of the diet was gleaned (Shiel et al. 1991). This species emerges late in the evening (median 55 mins after sunset) (Entwistle et al. 1996), as do *Myotis natteri*, which are also known to glean (Swift 1997, Swift and Racey 2002). In contrast the emergence time recorded for *R. hipposideros* recorded in my study is similar to bats that are known to feed on swarming insects using aerial hawking, such as *Pipistrellus pipistrellus* (35 mins after sunset) (Swift 1980). Species that appear to be adapted primarily for manoeuvrable flight in clutter, such as *R. hipposideros*, may be able to reduce foraging flight costs by flying in insect concentrations that form outside cluttered areas (Aldridge and Rautenbach 1987). Therefore I postulate dusk and dawn to be important foraging times for *R. hipposideros* with the majority of prey likely to be caught by aerial hawking within or adjacent to the canopy during at these times.

I determined that *R. hipposideros* exhibited multimodal patterns of activity through the night with a mean range of 2.6-5.5 flying bouts, interspersed with periods of roosting. I found the first flying bout to be significantly longer than both the final and in-between bouts. McAney and Fairley (1988b) also found an overnight decrease in activity. One of the few significant differences among landscapes in my study was that the length of the first flying bout was significantly longer in the lowland landscape compared with the high quality and upland types. If the period after dusk is an important foraging period then the data suggest that bats are feeding more efficiently in the high quality and upland landscapes, either as a result of higher biomass of suitable prey or a greater abundance of nutrient rich, profitable prey. Furthermore I found that during late pregnancy the bats in the high quality and upland landscapes spent less time foraging during the night and individual foraging bouts were shorter, compared with bats in the lowland landscape. My findings are in accordance with optimum foraging models (Stephens and Krebs 1986), whereby poor habitat quality would imply that bats would use larger foraging areas and/or spend longer time foraging.

Implications for conservation

The assessment of dispersal in relation to the main roads surrounding the lowland roost implied that the roads were not restricting movement. However it must be stressed that the roads in question are long-established. Current research suggests that new highway schemes can have a range of detrimental impacts on bats, principally loss of habitat and severance of flight lines (Limpens and Kapteyn 1991, Bach et al. 2004). Associated roadside lighting is also likely to adversely affect *R. hipposideros*. Their avoidance of lighting has been demonstrated and the species has not been recorded foraging around streetlights (Arlettaz et al. 2000) unlike some vespertilionid species (Rydell 1992, Blake et al. 1994). In addition, *R. hipposideros* road traffic casualties have been recorded on trunk roads, with a recent casualty also on a minor unclassified road (CatherineBickmoreAssociates 2003). Evidence for the vulnerability of the species to traffic strike was further recorded in the lowland landscape. An adult female (tracked the previous year) was killed along the main road outside the maternity roost and a juvenile (not

tagged) was seen to be hit by a lorry (pers. obs.). Therefore research is required to fully assess the affect of roads, and new trunk roads in particular, on the species.

For many species protecting adequate and connected habitat will be the single most important way to ensure long-term survival (Mackinnon 2000). This study has highlighted that the ranging behaviour of radio-tracked *R. hipposideros* was remarkably consistent within the three contrasting landscapes. Given that a mean maximum distance of 2 km was identified within each it is recommended that habitat within this radius around maternity roosts of the species be protected and enhanced where possible. This area can be classified as the 'roost sustenance zone' (Ransome 1996), which has been used successfully to target conservation measures for *R. ferrumequinum* (Longley 2003). However it is also important that the wider landscape should also be taken into account to aid gene flow. Although this study has demonstrated the relatively sedentary nature of *R. hipposideros* during the breeding season, the distances between winter and summer quarters are greater, between 5-10 km (Mitchell-Jones et al. 1999) and 27 km (Gaisler and Chytil 2002), although the species is known to migrate long distances, exceeding 146 km (Harmata 1989).

CHAPTER FOUR

ROOSTING BEHAVIOUR OF *R. HIPPOSIDEROS*

4 Roosting behaviour of *R. hipposideros*

4.1 *Summary*

I examined the behaviour of *R. hipposideros* during the breeding season by using radio-telemetry. 64 roost sites in addition to the maternity roosts were located for 54 individuals.

One-third to two-thirds of the bats used alternative day roosts, which were a mean distance of 1.15–1.26 km from the maternity roost. Roost switching was most frequently recorded in nulliparous females and in breeding females during early pregnancy and post-lactation, with greater philopatry observed in lactating females and juveniles. Overall mean weather conditions during the previous night and at dawn were not found to affect choice of roosting location.

The bats exhibited multimodal patterns of overnight activity with between one and eight night roosting bouts (mean 2.1–4.5). I suggest that *R. hipposideros* deviates from the more typical bimodal pattern shown by many insectivorous bat species as their broad diet allows them to feed throughout the night. Over 75 % of the bats night roosted away from the maternity roost, typically in buildings. Up to five different night roosts were used by individual bats with the number of night roosts significantly correlated with home range, core area and range span. Night roosts were on average 1.3–2.4 km from the maternity roost and were significantly nearer to core areas, with 56–64% actually contained within cores.

The multimodal activity pattern and frequent use of night roosts, and alternative day roosts, is an important aspect of *R. hipposideros* behaviour and needs to be considered carefully when designing management strategies to conserve the species. I postulate that minimisation of distance to feeding sites may be the primary function of the night roosts, being used for resting and digestion between foraging bouts. As such they may form an integral part of the core foraging areas and need to be protected.

4.2 *Introduction*

Bats spend a large proportion of their lives roosting, and a wide diversity of roosting behaviours are found in insectivorous bats (Kunz 1982, Altringham 1996, Kunz and Lumsden 2003). Those at high latitudes tend to roost in larger groups, following a refuging system (Kunz 1982), using a central maternity roost to give birth and raise their young, and from which they forage. The selection of appropriate roost conditions during the day may be essential in balancing the energy budget of bats and have important implications for survival and fecundity (Kunz 1982). An understanding of their roosting ecology is therefore fundamental to their conservation and information on the pattern of roost use is essential to develop reasonable management plans (Kunz and Lumsden 2003).

The roosting ecology of *R. hipposideros* has been, in part, well studied. In Britain the species generally roosts in buildings during the summer and uses caves and mines during the hibernation period. Although the use of night roosts by *R. hipposideros* has been previously highlighted (Gaisler 1963c, McAney and Fairley 1988a, Schofield 1996), research has focussed on maternity roosts and hibernation sites. For example, within Britain the general characteristics of *R. hipposideros* maternity roosts have been well documented (McAney and Fairley 1988a, Schofield 1996) and on-going monitoring of colony counts at maternity roosts and hibernation sites is widespread (Warren and Witter 2002). However, very much less is known about use of alternative roosts for day and night roosting.

Early studies of overnight activity of the species failed to describe any overall pattern (Gaisler 1963c, McAney and Fairley 1988a, Schofield 1996). However in Chapter 3 I determined that *R. hipposideros* exhibits multimodal patterns of activity through the night with a mean range of 2.6-5.5 flying bouts, interspersed with periods of roosting. This multimodal pattern is unusual. A review by Erkert (1982) found that insectivorous bats characteristically follow a bimodal pattern of activity with peaks around dusk and dawn. Bimodal patterns with two peaks in 24-hr are the commonest type of daily rhythms among animals but if environmental stimuli are removed the second peak may disappear (Aschoff 1966). For example, in *Pipistrellus* sp. the dawn peak occurs during lactation but is otherwise

suppressed (Swift 1980, Maier 1992). The unusual multimodal pattern exhibited by *R. hipposideros* therefore warrants further study and may suggest that night roosting behaviour is of greater importance to the species than previously highlighted.

I examined the roosting behaviour of *R. hipposideros* within three distinct landscape types in Britain by using radio-telemetry to determine whether spatial and seasonal variation exists.

The specific aims of this chapter are:

1. To describe roosting behaviour, including proportion of time spent roosting in the maternity roost or alternative roosts, relationships among night roosts and core home ranges and density of alternative roosts.
2. To test whether roosting behaviour varies across different landscape types in Britain.
3. To determine any changes in roosting behaviour according to reproductive status.
4. To describe any similarities between my study and previous research into the roosting behaviour of *R. hipposideros.*
5. To investigate the link between roosting behaviour and the foraging behaviour as described in Chapter 3.

4.3 *Methods*

4.3.1 Study sites, capture of bats and tagging procedure

Bats were radio-tracked from three maternity roosts during the summer of 2003, 2004 and 2005. The roosts represented the key landscape types that characterise the distribution of *R. hipposideros* in Britain: lowland (Roost A, North Somerset), a high quality landscape (Roost B, Wye Valley, Gloucestershire and Monmouthshire) and upland (Roost C, Powys). For descriptions of study sites refer to Section 2.3.1, Chapter 2. The study was undertaken during early to late May (early pregnancy), late May to early June (late pregnancy), late July to mid-August (lactation) and late August to mid-September (post-lactation).

For full details of capture of bats and tagging procedure, refer to Section 3.3.1, Chapter 3.

4.3.2 Radio-tracking equipment and data collection

Bats were followed continuously and fixes (the determined or estimated locations of the tagged individual) were recorded at 15 min intervals as six-figure grid references (±100 m). An activity category was assigned to each fix: commuting (rapid, directional movements between distant sites), foraging (sustained activity within a defined area of variable size), perching (typically a period of inactivity <10 min where the bat was hanging from a tree), night roosting (typically a period of inactivity >10 min within a building or other structure) or day roosting. Flying bouts commenced on emergence from the day roost around dusk and comprised commuting, foraging and perching behaviour and were typically interspersed with night roosting bouts through the night.

For full details of equipment used and methods of data collection refer to Section 3.3.2, Chapter 3.

4.3.3 Data analysis

Home-range analyses were undertaken using the Ranges 6 v1.2 (Kenward et al. 2003) and Ranges 7 v1.0 analysis system (South and Kenward 2006) (Anatrack Ltd., Wareham, UK). The 'study area' is defined as a maximum range circle (MRC) centred on the roost site, containing all of the fixes of the radio-tracked bats from the colony. Home ranges were calculated as 100 % minimum convex polygons (MCPs) (Mohr 1947) of all fixes and range span was calculated from the maximum width of the 100 % MCPs. I then used cluster analysis (Kenward 1987, 2001) to remove outlying fixes and describe core areas (Harris et al. 1990). I created 85 % cluster cores using only commuting, foraging and perching fixes (i.e. omitting day roosting and night roosting fixes from the data set), hereafter termed as 'active core' areas. As commuting (excursive activity) fixes are generally removed by the use of cluster cores the active cores typically represent core

foraging areas. This therefore allows comparison between core foraging areas and night roost locations. The active cores consisted of a number of nuclei (i.e. separate groups of fixes), hereafter termed active core nuclei. The number of nuclei within the active core areas was also recorded.

Patterns of distributions of additional roosts around the maternity roost were analysed using circular statistics (Batschelet 1981, Zar 1999). Correlations between different response variables were tested using the non-parametric Spearman's rank-order correlation (Dytham 1999). General Linear Modelling (GLM) was used to analyse the radio-tracking data. The following response variables were tested: proportion of time spent day roosting away from the maternity roost, mean number of night roosts used, mean number of night roosting bouts per night, mean length of average night roosting bout, mean length of first night roosting bout, overall number of nuclei in active core, minimum distance between the night roosts and nearest nucleus, minimum distance between the maternity roost and nearest nucleus and maximum distance between the maternity roost and furthest nucleus. The mean value of the first five response variables over the number of nights that each bat was tracked (refer to Table 3.1, Chapter 3) was used to avoid pseudoreplication. For the remaining response variables the overall value (using all fixes collected) was used. Explanatory variables were breeding status and locality (categorical variables) and, where appropriate, temperature, rainfall, wind speed and cloud cover at return, and minimum night temperature, average nightly rainfall and average nightly wind speed (continuous variables). Multiple comparisons among the means of significant categorical explanatory variables were undertaken using Tukey's method.

For full details of the GLM methods, including the model simplification process and assumptions of the GLM, refer to Section 3.3.3, Chapter 3. All statistical analyses were carried out on Minitab version 13.32 for Windows (Minitab, Coventry, UK) with a significance level of 5 %.

4.4 Results

During the three year study (2003-5) data were obtained from 54 *R. hipposideros* fitted with radio-transmitters (refer to Table 3.1, Chapter 3, for sampling effort). Within the lowland landscape, a total of 36 bats were radio-tracked: 6 adult females in early pregnancy, 6 adult females in late pregnancy, 6 adult females during lactation, 6 adult females during post-lactation, 6 nulliparous females and 6 juveniles (2 females, 4 males). A further 18 bats were tracked in the high quality and upland landscapes (3 adult females in late pregnancy, 3 adult females during lactation and 3 adult females during post-lactation at each locality).

A total of 64 additional roosting sites were identified during the radio-tracking study. Details are provided in Appendix 2.

Alternative roosts were predominantly within a wide variety of man-made structures, of varying build and ages (Table 4.1): outbuildings associated with domestic properties (n = 18), old barns (n = 10), garages (n = 9; Plate 4.1), stables (n = 3) and a porch (n = 1). A further 4 roosts were in derelict buildings, 2 of which were ruins with no roof intact (one a small cottage, Plate 4.2; the other a former manor) and the bats were located roosting in the chimney.

Seven barns were two-storey whereas other buildings were typically single-storey. Roof structure was varied and included flat felt roofs (on garages and outbuildings) and sloping or pitched tiled / slate / corrugated iron roof. A feature of all of the buildings was their open-aspect, with an often sizeable opening ranging from an open window / doorway to open front.

A further 9 roosts were in underground structures: caves / mines (n = 3), cellars (n = 3), former railway tunnel (n = 1), former lime kiln (n = 1; Plate 4.3) and a small open structure in a stone faced bank associated with a former quarry (n = 1).

Plate 4.1. Garage used as night roost by *Rhinolophus hipposideros*.

Plate 4.2. Chimney of derelict cottage used as day roost and night roost by *Rhinolophus hipposideros*.

Plate 4.3. Former lime kiln used as a night roost by *Rhinolophus hipposideros*. At 04:32 on 14/9/2004 5 bats were night roosting in left side.

Structure	Day roost			Night roost		
	Lowland	High quality	Upland	Lowland	High quality	Upland
Barn	2		3	4	1	5
Stables		1			1	1
Garage	3			8	1	
Outbuilding of domestic property	8	1	2	9	3	3
Porch				1		
Underground structure	2	2	1		6	
Derelict property		2	1	1	2	
Tree	1			2		
Unidentified				4		3
Total recorded	16	6	7	29	14	12

Table 4.1. Use of different types of alternative roosts recorded when radio-tracking *Rhinolophus hipposideros* in three contrasting landscape types: lowland (n = 36 bats), high quality (n = 9 bats) and upland (n = 9 bats).

Roosting in trees was seldom recorded (n = 3) and was restricted to the lowland landscape. A nulliparous female day roosted in a mature standard small-leaved lime *Tilia cordata*. I did not identify any large cavities during a day time inspection of the tree and I assumed the bat was roosting among dense outgrowths from the trunk. The same bat also night roosted in a mature standard ash *Fraxinus excelsior* tree. Both instances occurred on a night of persistent moderate/heavy rainfall (see also Section 4.4.1. below). A lactating female was also recorded night roosting in a mature standard pedunculate oak *Quercus robur* tree during heavy rain.

Given that a large proportion of the roosts are within man-made structures it is not surprising that 83 %, 67 % and 79 % of the roosts occur within the 'settlement' habitat type (see Chapter 5 for definition) in the lowland, high quality and upland landscapes respectively. Other habitats types (coniferous and mixed woodland,

and pasture with unmanaged hedgerow) were seldom represented except broad-leaved woodland in which 11 % of the lowland and 26 % of the high quality roosts occurred. These roosts were typically trees or underground sites. The distribution of the roosts in the three landscape types in relation to the settlement habitat type is given in Figure 4.1.

In the lowland landscape 35 additional roosts were recorded. One roost (barn) I identified during the study was found to support 45 bats, including mothers with young. In addition owners of three other roosts (3 outbuildings, 2 of which are used as boiler rooms) reported that they had observed 'large numbers' of bats and past breeding activity, although no more than 15 bats were recorded during the tracking period and no breeding activity seen (refer to Appendix 2 for details). It is likely that these roosts were used as satellite roosts when the maternity roost barn was undergoing conversion in the previous decade.

Circular statistics indicated that the 35 roosts were not uniformly distributed about the maternity roost (circular statistics, $\chi^2 = 49.17$, d.f. = 5, $p < 0.001$). Day roosting was recorded in 16 of the roosts and night roosting in 29 roosts. These day and night roosts were also not uniformly distributed about the maternity roost (circular statistics, $\chi^2 = 6.50$, d.f. = 2, $p < 0.05$; $\chi^2 = 34.28$, d.f. = 4, $p < 0.001$ respectively).

15 alternative roosts were identified in the high quality landscape. 6 of the roosts were used as day roosts and 14 for night roosting. The 15 roosts were uniformly distributed about the maternity roost (circular statistics, $\chi^2 = 5.20$, d.f. = 2, NS).

In the upland landscape 14 additional roosts were noted. 7 were used for day roosting and 12 as night roosts. The 14 roosts were not uniformly distributed about the maternity roost (circular statistics, $\chi^2 = 14.00$, d.f. = 1, $p < 0.001$).

Figure 4.1a overlay. The distribution of the active core nuclei (—) in the lowland landscape around the maternity roost (●).

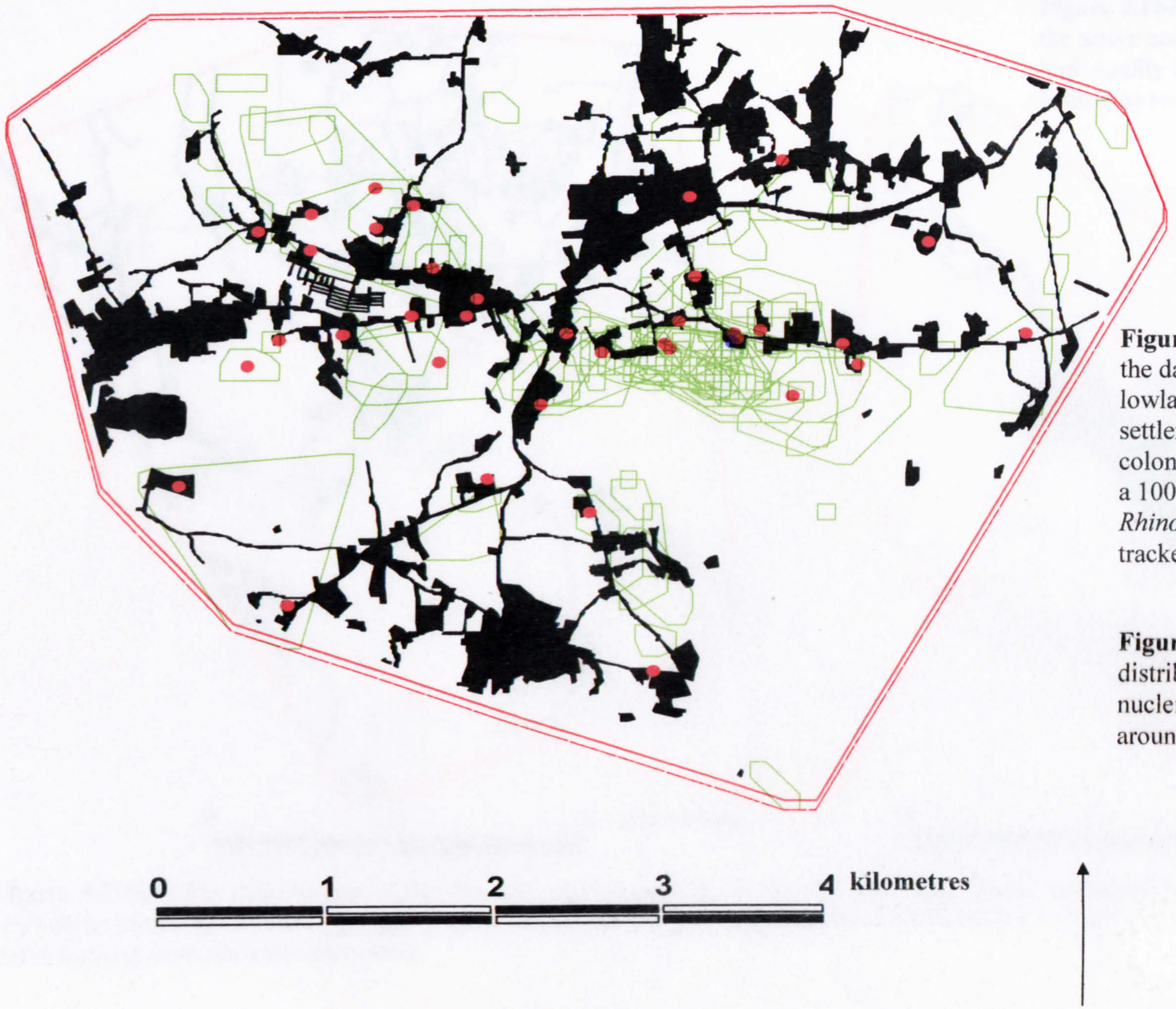

Figure 4.1a. The distribution of the day and night roosts (●) in the lowland landscape in relation to settlement habitat type (■). The colony home range is delimited by a 100% MCP (—) of fixes from all *Rhinolophus hipposideros* radio-tracked from the maternity roost.

Figure 4.1a overlay. The distribution of the active core nuclei (—) in the lowland landscape around the maternity roost (●).

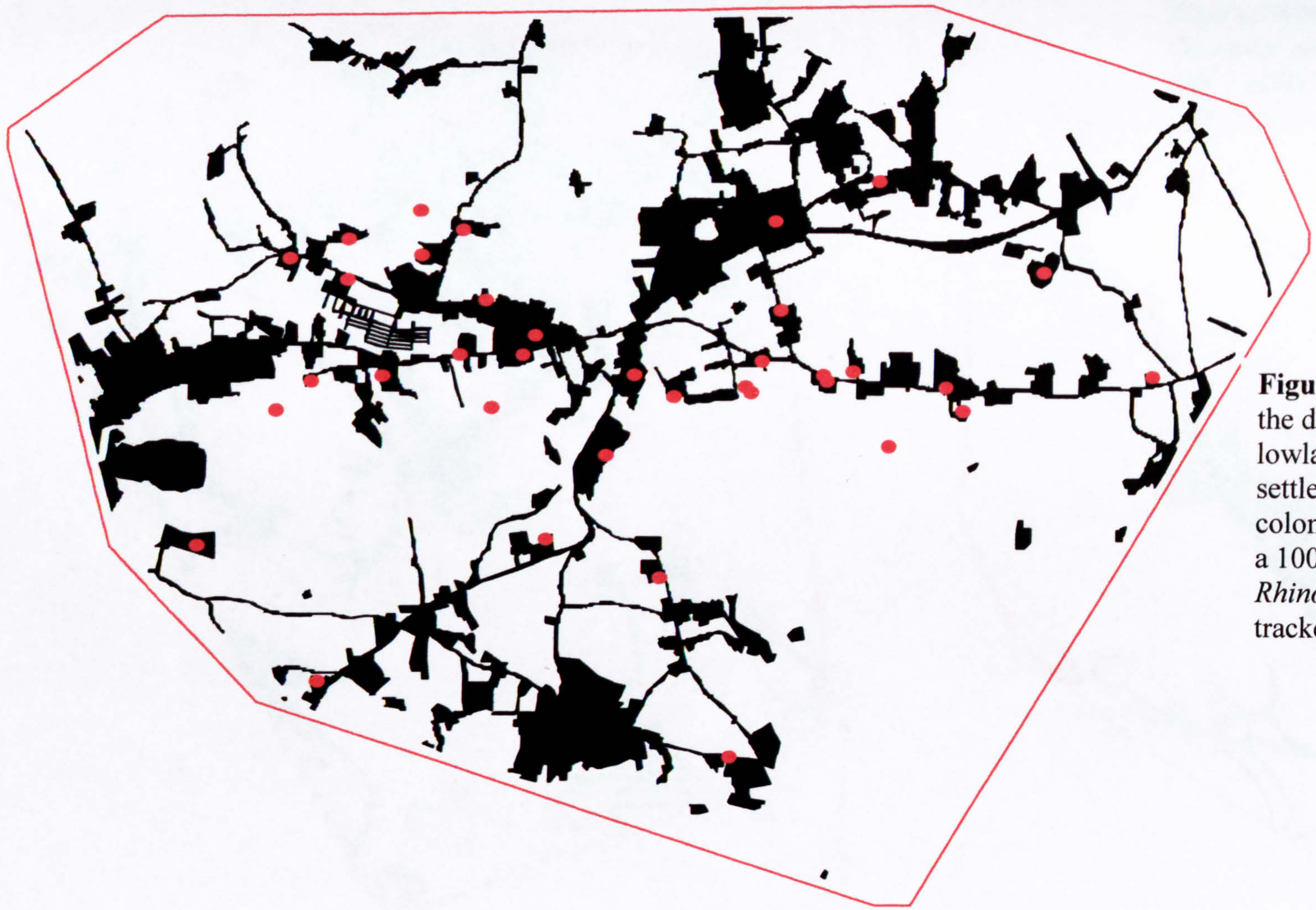

Figure 4.1a. The distribution of the day and night roosts (●) in the lowland landscape in relation to settlement habitat type (■). The colony home range is delimited by a 100% MCP (—) of fixes from all *Rhinolophus hipposideros* radio-tracked from the maternity roost.

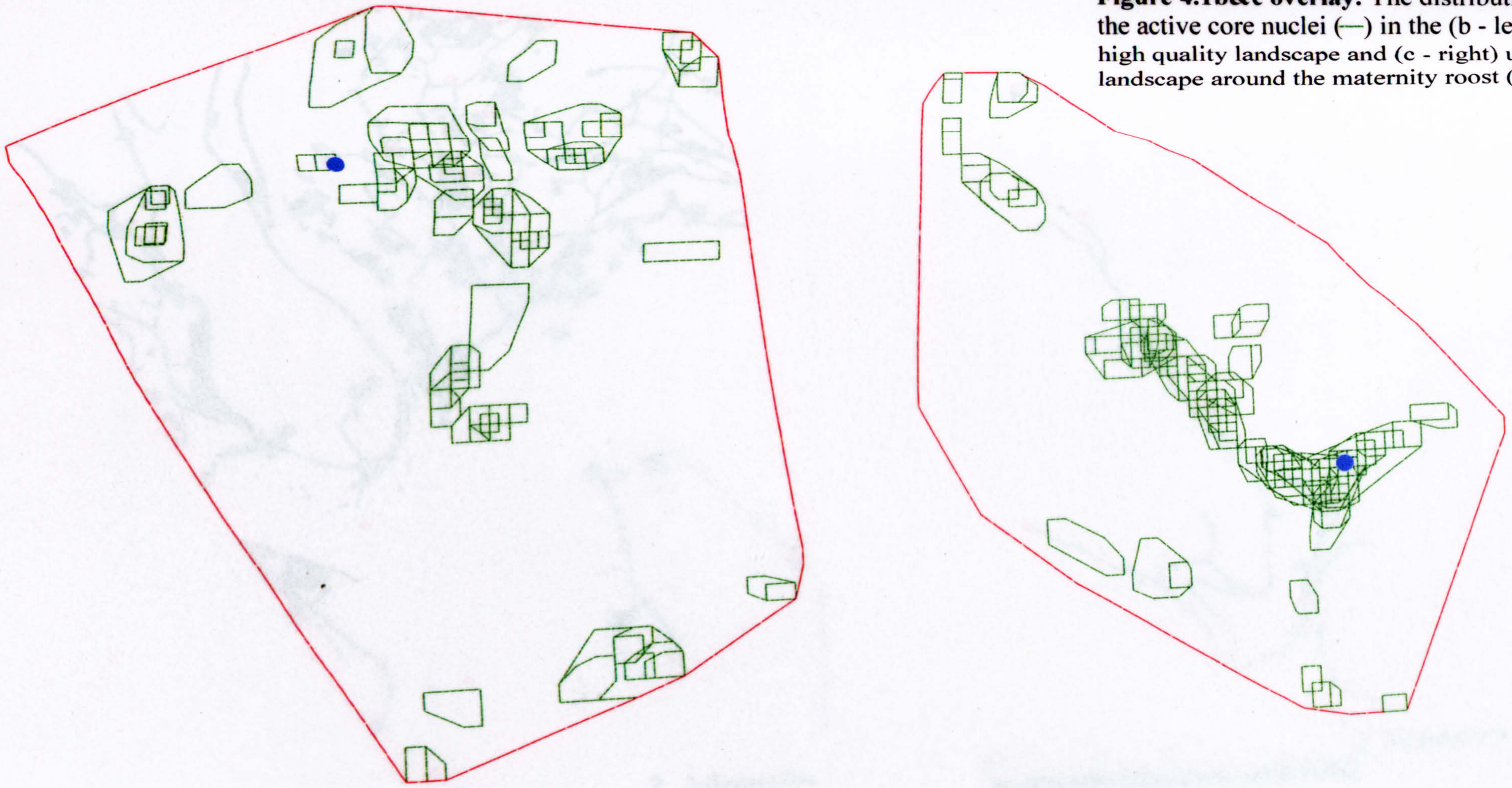

Figure 4.1b&c overlay. The distribution of the active core nuclei (—) in the (b - left) high quality landscape and (c - right) upland landscape around the maternity roost (●).

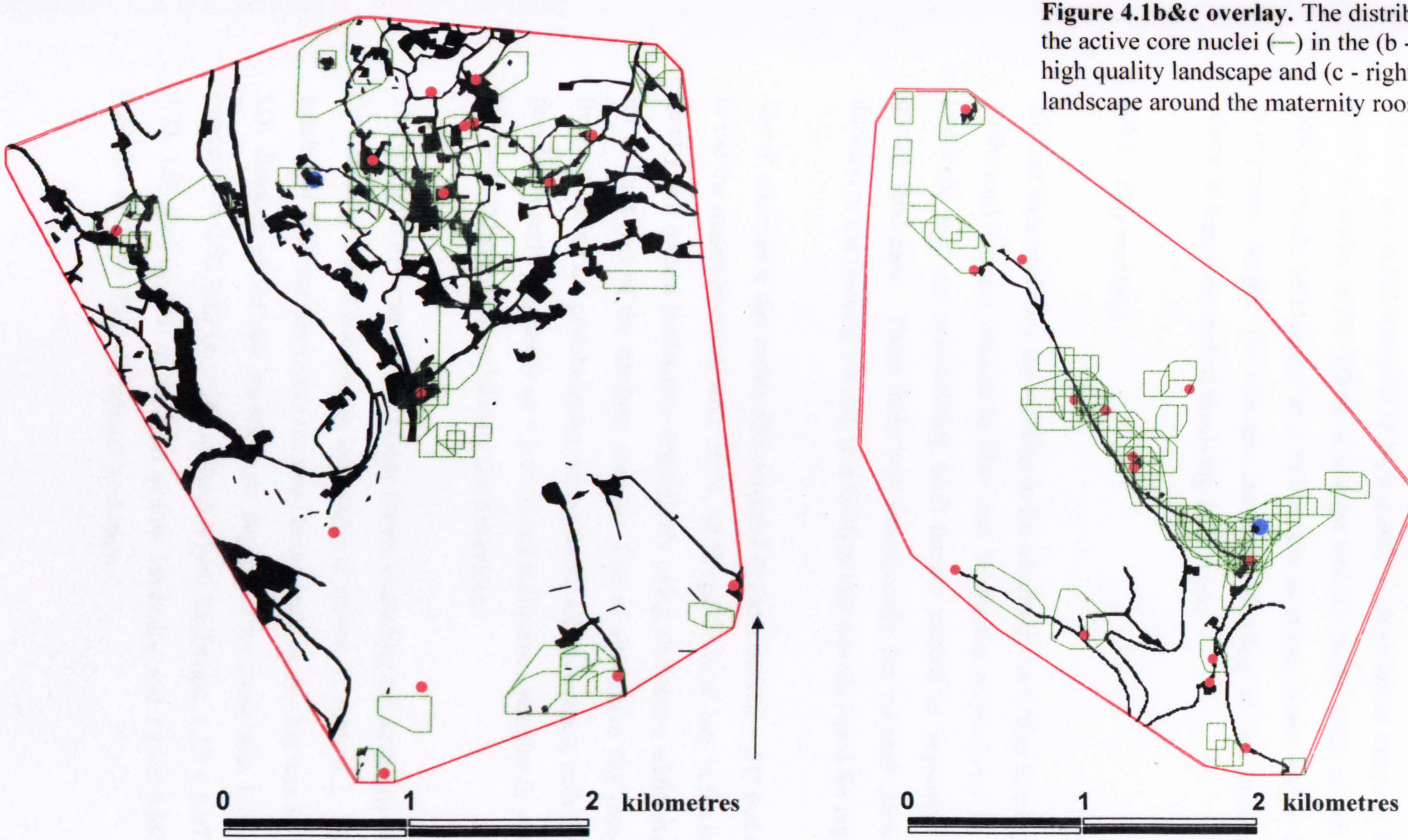

Figure 4.1b&c overlay. The distribution of the active core nuclei (—) in the (b - left) high quality landscape and (c - right) upland landscape around the maternity roost (●).

Figure 4.1b&c. The distribution of the day and night roosts (●) in the (b - left) high quality landscape and (c - right) upland landscape in relation to settlement habitat type (■). The colony home range is delimited by a 100% MCP (—) of fixes from all *Rhinolophus hipposideros* radio-tracked from the maternity roost.

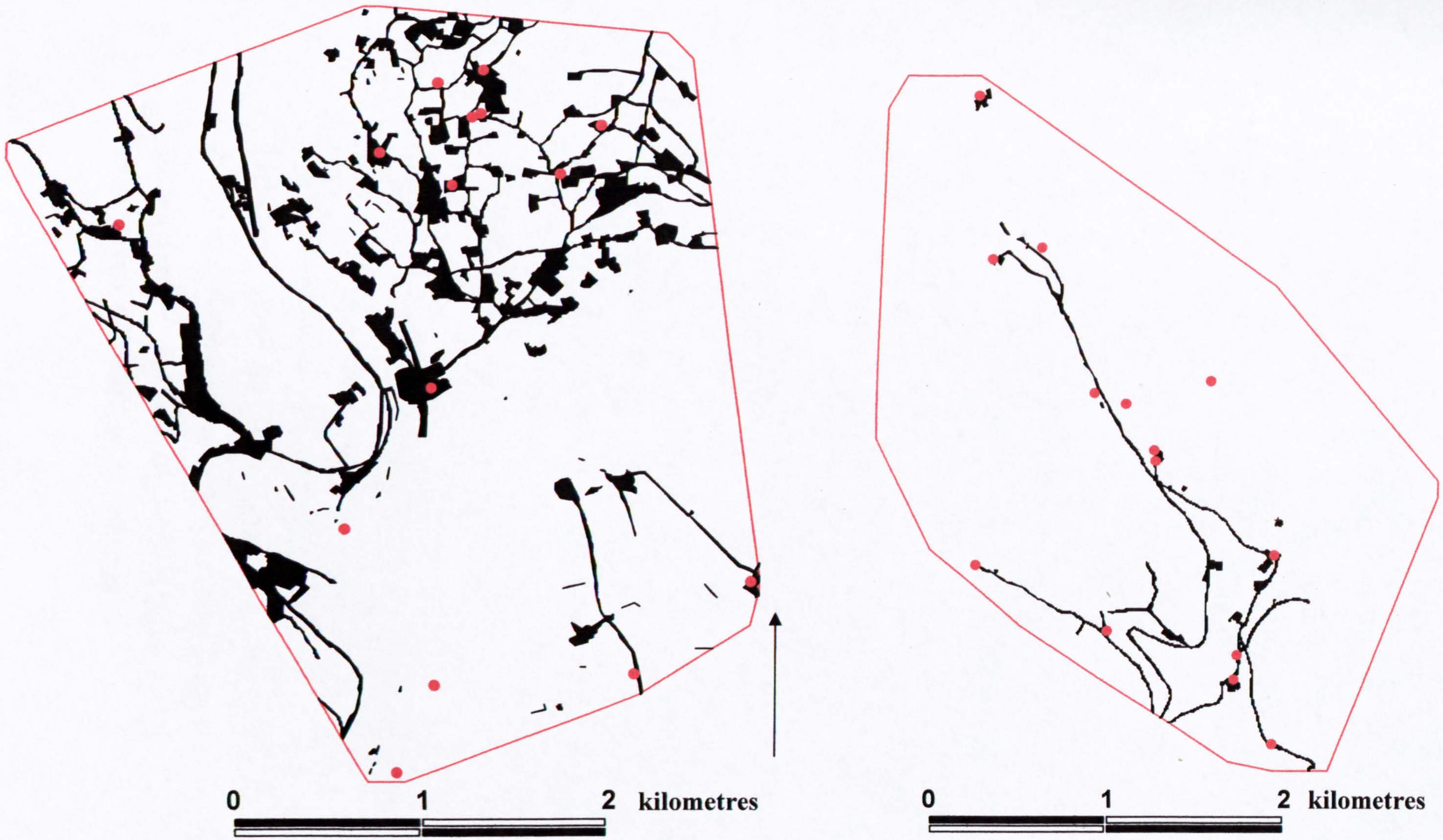

Figure 4.1b&c. The distribution of the day and night roosts (●) in the (b - left) high quality landscape and (c - right) upland landscape in relation to settlement habitat type (■). The colony home range is delimited by a 100% MCP (—) of fixes from all *Rhinolophus hipposideros* radio-tracked from the maternity roost.

The density of the roosts compared with the colony home range (determined by all fixes collected per landscape) was 0.014 roosts/ha in lowland (colony home range of 2485 ha), 0.012 roosts/ha in high quality (colony home range of 1246 ha) and 0.017 roosts/ha in the upland landscape (colony home range of 809 ha). These figures should be regarded as a mimumum as colony home ranges do not reach asymptotes, despite for example intensive sampling at the lowland landscape where 36 bats were studied involving 2124 fixes.

4.4.1 *Day roosting*

All bats were recorded day roosting in the maternity roost after tagging, except two nulliparous females tracked in May and September respectively in the lowland landscape and one post-lactating adult female tracked in September in the high quality landscape. These three bats subsequently day roosted elsewhere for the duration of the tracking session, in a location that was also used for night roosting.

Use of alternative day roosts also occurred in those bats (n = 51) that did continue to use the maternity roost, with 50 %, 38 % and 67 % of bats in the lowland, high quality and upland landscapes respectively using alternative additional day roosts for at least part of the tracking session. Use of alternative day roosts was most frequent during the post-lactation period across all landscapes, with the majority of females in early pregnancy (n = 5 of 6) and nulliparous females (n = 3 of 4) in the lowland landscape also exhibiting this behaviour.

The variation in mean number of day roosts, excluding the maternity roost, through the breeding season and among landscapes is shown in Table 4.2. The maximum number of different day roosts recorded being used by any bat was 3. The mean (± SD) distance of the day roosts from the maternity roost was 1.26 ± 0.837 km (range 0.16–2.92 km) (n = 16) in the lowland landscape, 1.19 ± 0.973 km (range 0.32–3.05 km) (n = 6) in the high quality landscape and 1.15 ± 0.695 km (range 0.20–2.6 km) (n = 7) in the upland landscape.

The general linear model (GLM) showed that proportion of use of alternative day roosts (arcsine transformed) did not vary between landscapes (GLM, $F_{2,46} = 1.73$, NS) but was affected by breeding status (GLM, $F_{5,46} = 6.44$, $p < 0.001$). Multiple comparisons for status indicated that nulliparous females were significantly less likely to day roost in the maternity roost than juveniles and lactating females. Covariates and all interaction terms were removed during model simplification. The average night time and dawn weather conditions had no effect on use of alternative day roosts.

However field data suggest that weather conditions did occasionally impact temporarily on the bats' behaviour. For example, on two occasions involving a lactating female and a nulliparous female, heavy rain prior to dawn appeared to inhibit movement of the tracked bat back to the maternity roost (pers. obs.). The lactating female day roosted in a night roost and the nulliparous female started to commute back to the maternity roost before stopping and day roosting in a tree. In another instance a prolonged distant electric storm curtailed activity of all six tagged bats, despite no rainfall. On two occasions roost switching during the daytime was also recorded (pers. obs.).

	Mean number of day roosts (excluding maternity roost) per bat			Mean number of night roosts (excluding maternity roost) per bat			Total number of alternative roosts (excluding maternity roost) per bat		
	Lowland	High quality	Upland	Lowland	High quality	Upland	Lowland	High quality	Upland
Adult female									
Early pregnancy	0.8±0.4			1.2±0.4			1.5±0.8		
Late pregnancy	0.3±0.5	0.7±0.6	0.7±1.2	1.2±1.2	1.0±0.0	1.7±1.5	1.5±1.2	1.3±0.6	2.3±0.6
Lactation	0.2±0.4	0.0±0.0	0.3±0.6	1.5±1.4	1.0±1.7	2.0±1.7	1.3±1.4	1.0±1.7	2.0±1.7
Post-lactation	1.2±0.8	1.3±0.6	1.3±0.6	1.2±0.4	2.7±2.1	1.7±0.6	1.7±0.5	2.7±2.1	2.0±1.0
Nulliparous female	1.2±1.0			1.5±0.5			1.7±0.8		
Juvenile	0.2±0.4			0.7±0.8			0.8±1.2		
Overall (adults only)	0.6±0.6	0.7±0.7	0.8±0.8	1.3±0.9	1.6±1.6	1.8±1.2	1.5±1.0	1.7±1.6	2.1±1.1

Table 4.2. Mean number of day and night roosts recorded for *Rhinolophus hipposideros* radio-tracked in three different landscapes. Values are means ±1 SD. Within the lowland landscape, a total of 36 bats were radio-tracked: 6 adult females in early pregnancy, 6 adult females in late pregnancy, 6 adult females during lactation, 6 adult females during post-lactation, 6 nulliparous females and 6 juveniles (2 females, 4 males). A further 18 bats were tracked in the high quality and upland landscapes (3 adult females in late pregnancy, 3 adult females during lactation and 3 adult females during post-lactation at each locality).

4.4.2 *Night roosting*

The majority of bats were recorded night roosting in one or more locations away from the maternity roost. In the lowland landscape night roosting activity was restricted to the maternity roost in only 6 bats (2 females in late pregnancy, 1 lactating female and 3 juveniles). 2 bats in the high quality (2 lactating females) and 2 bats in the upland landscape (1 female in late pregnancy and 1 during lactation) also only night roosted in the maternity roost.

Night roosts were checked on only two occasions. On the first check I found bats did not tolerate the disturbance and exited the roost. Therefore I decided to avoid potentially disrupting their activity pattern in this way. At one night roost (barn, during lactation) two bats were present (including the study individual). At another roost (lime kiln, during post-lactation and during a night of heavy rain showers) 5 bats were present (excluding tagged bat which was flying nearby). Further evidence of use by a range of individuals was gained through the radio-tracking, particularly at the lowland locality where work was more intensive, and roosts were used by up to 6 different tagged bats.

The mean (± SD) distance of the night roosts from the maternity roost was 1.71 ± 0.980 km (range 0.03–3.44 km) ($n = 29$) in the lowland landscape, 2.40 ± 1.440 km (range 0.32–3.50 km) ($n = 14$) in the high quality landscape and 1.34 ± 0.860 km (range 0.82–3.05 km) ($n = 12$) in the upland landscape.

The variation in number of night roosts, excluding the maternity roost, through the breeding season and among landscapes is provided in Table 4.2. The maximum number of different night roosts recorded being used by any bat was 5. The number of night roosts (square root transformed) did not vary between landscapes (GLM, $F_{2,46} = 0.89$, NS) or according to breeding status (GLM, $F_{5,46} = 0.32$, NS).

There was a positive correlation between the number of night roosts used (excluding and including the maternity roost) and the home range (100 % MCP) (non-parametric Spearman's rank-order correlation, $r_s = 0.403$, $p < 0.01$; $r_s = 0.416$,

$p < 0.01$ respectively). There was also a positive correlation between the number of night roosts used (excluding and including the maternity roost) and the size of the active cores (non-parametric Spearman's rank-order correlation, $r_s = 0.316$, $p < 0.05$; $r_s = 0.405$, $p < 0.01$ respectively). Furthermore there were also positive correlations between the number of night roosts used (excluding and including the maternity roost) and the range span (based on 100 % MCP) (non-parametric Spearman's rank-order correlation, $r_s = 0.302$, $p < 0.05$; $r_s = 0.308$, $p < 0.05$ respectively). This is unsurprising given that there is a strong positive correlation between the home range size and both active core and range span (non-parametric Spearman's rank-order correlation, $r_s = 0.758$, $p < 0.001$; $r_s = 0.914$, $p < 0.001$ respectively).

Active cores comprised 4.1±2.54 nuclei (range 1 – 12). The number of nuclei within the active cores (log transformed) did not vary between landscapes (GLM, $F_{2,46} = 0.86$, NS) but was affected by breeding status (GLM, $F_{5,46} = 3.69$, $p < 0.01$). Juveniles had the greatest number of nuclei and multiple comparisons for status indicated that number of nuclei was significantly smaller for females in early and late pregnancy and for nulliparous females compared with juveniles.

There was no correlation between the number of night roosts used (excluding and including the maternity roost) and the number of nuclei within the active cores (non-parametric Spearman's rank-order correlation, $r_s = 0.020$, NS; $r_s = 0.033$, NS respectively).

The distribution of the night roosts in the three landscape types in relation to the nuclei in the active cores (Figure 4.1 overlay) shows that, overall, night roosts were contained predominantly within the active cores of all bats. Individually 58 %, 64 % and 56 % of night roosts were contained within active cores within the lowland, high quality and upland landscape respectively. The distances of the nearest active core nuclei from night roosts are provided in Table 4.3, together with the distances of the nearest and furthest nuclei from the maternity roost. The minimum distance of the nuclei within the active core from night roosts is significantly smaller than the minimum distance of the active core nuclei from the maternity roost (Wilcoxon's signed ranks test = 572.5, $p < 0.05$).

The minimum distance between the night roosts and nearest nucleus did not vary between landscapes (GLM, $F_{2,36} = 0.53$, NS) and was not affected by breeding status (GLM, $F_{5,36} = 0.93$, NS). However the minimum distance between the maternity roost and nearest nucleus (log transformed) did vary between landscapes (GLM, $F_{2,46} = 5.93$, $p < 0.01$) and was affected by breeding status (GLM, $F_{5,46} = 3.57$, $p < 0.01$). Multiple comparisons for locality indicated that the minimum distance was significantly greater in the high quality landscape than in the lowland and upland areas. Multiple comparisons for status indicated that minimum distance was significantly smaller in juveniles compared with females in early pregnancy and post-lactation.

The maximum distance between the maternity roost and active core nuclei did not vary between landscapes (GLM, $F_{2,46} = 0.43$, NS) and was not affected by breeding status (GLM, $F_{5,46} = 2.10$, $p = 0.08$).

Night roosting bouts

The bats showed multimodal phases of activity during the night (Chapter 3). There were between one and eight night roosting bouts (mean range 2.1–4.5, depending on locality and reproductive status, refer to Table 4.4). Night roosting bouts lasted on average 76-81 min (Table 4.5). In general the bats emerged from the night roost before dawn for the final flying bout, except for 9 % of the time in which they remained night roosting through to dawn.

	Distance of NR from nearest nuclus/m			Distance of MR from nearest nucleus/m			Distance of MR from furthest nucleus/m		
	Lowland	High quality	Upland	Lowland	High quality	Upland	Lowland	High quality	Upland
Adult female									
Early pregnancy	42±65.2			443±639.5			1475±663.1		
Late pregnancy	254±308.4	13±23.1	173±193.3	110±130.2	230±239.0	57±98.1	1022±1030.6	763±340.3	827±631.2
Lactation	81±83.7	50±0.0	190±94.3	73±96.3	410±302.0	0.0±0.0	1633±1310.1	1450±615.4	1120±294.6
Post-lactation	119±199.4	91±116.7	3±5.8	687±1083.2	940±626.4	103±76.4	1712±928.1	2753±922.0	1827±1193.2
Nulliparous female	28±28.4			300±374.9			1273±1189.2		
Juvenile	15±26.0			0.0±0.0			905±590.3		
Overall (adults only)	115±179.7	52±78.9	105±129.8	328±645.0	527±487.2	53±76.6	1460±980.5	1656±1050.0	1258±821.8

Table 4.3. Distance of edge of nearest nucleus in active cores from night roosts (NR) and the maternity roost (MR) for *Rhinolophus hipposideros* radio-tracked in three different landscapes. Values are means ±1 SD. Within the lowland landscape, a total of 36 bats were radio-tracked: 6 adult females in early pregnancy, 6 adult females in late pregnancy, 6 adult females during lactation, 6 adult females during post-lactation, 6 nulliparous females and 6 juveniles (2 females, 4 males). A further 18 bats were tracked in the high quality and upland landscapes (3 adult females in late pregnancy, 3 adult females during lactation and 3 adult females during post-lactation at each locality).

	Mean number of night roosting bouts			Mean number of flying bouts		
	Lowland	High quality	Upland	Lowland	High quality	Upland
Adult female						
Early pregnancy	2.1±0.58			2.6±0.69		
Late pregnancy	2.2±0.69	2.6±0.96	3.0±1.40	3.1±0.71	3.6±0.96	3.7±1.95
Lactation	2.8±0.95	2.6±0.67	3.9±0.42	3.5±0.90	3.6±0.67	4.9±0.42
Post-lactation	3.7±0.98	4.5±2.18	3.6±0.69	4.7±0.98	5.5±2.18	4.4±0.51
Nulliparous female	2.8±0.8			3.8±0.83		
Juvenile	2.8±0.61			3.8±0.72		
Overall (adults only)	2.7±1.00	3.2±1.57	3.5±0.9	3.5±1.09	4.2±1.57	4.4±1.17

Table 4.4. Mean number of night roosting and flying bouts recorded for *Rhinolophus hipposideros* radio-tracked in three different landscapes. Values are means ±1 SD. Within the lowland landscape, a total of 36 bats were radio-tracked: 6 adult females in early pregnancy, 6 adult females in late pregnancy, 6 adult females during lactation, 6 adult females during post-lactation, 6 nulliparous females and 6 juveniles (2 females, 4 males). A further 18 bats were tracked in the high quality and upland landscapes (3 adult females in late pregnancy, 3 adult females during lactation and 3 adult females during post-lactation at each locality).

	Lowland	High quality	Upland
Adult female			
Early pregnancy	100±34.9		
Late pregnancy	69±33.6	107±52.7	107±102.2
Lactation	84±56.6	58±23.4	47±9.6
Post-lactation	71±30.9	64±30.0	73±31.4
Nulliparous female	102±69.4		
Juvenile	85±53.3		
Overall (adults only)	81±39.6	76±40.0	76±59.7

Table 4.5. Length of average night roosting bout (mins) recorded for *Rhinolophus hipposideros* radio-tracked in three different landscapes. Values are means ±1 SD.

Number of night roosting bouts did not vary between landscapes (GLM, $F_{2,45}$ = 2.10, NS) but was affected by breeding status (GLM, $F_{5,45}$ = 2.46, $p < 0.05$). Multiple comparisons for status indicated that number of night roosting bouts was significantly smaller in early and late pregnancy compared with post-lactation. Average wind speed significantly affected number of bouts (GLM, $F_{1,45} = 7.71$, $p < 0.01$) with stronger winds associated with more bouts. Minimum temperature, average rainfall and all interaction terms were removed during model simplification. These results concur with the analysis of number of foraging bouts in Chapter 3.

Length of the first night roosting bout (log transformed) did vary between landscapes (GLM, $F_{2,44} = 5.39$, $p < 0.01$) but was not affected by breeding status (GLM, $F_{5,44} = 0.93$, NS). Multiple comparisons indicated that the length of the first night roosting bout was significantly shorter in the upland landscape and longest in the high quality landscape. It was affected by rainfall (inverse transformed) (GLM, $F_{1,44} = 5.00$, $p < 0.05$) but not wind speed (GLM, $F_{1,43} = 1.29$, NS) with increased rainfall associated with a shorter first night roosting bout. Minimum temperature and interaction terms were removed during model simplification.

Length of the average night roosting bout (log transformed) did not vary between landscapes (GLM, $F_{2,43} = 0.48$, NS) and was not affected by breeding status (GLM, $F_{5,43} = 1.75$, NS) or minimum air temperature (GLM, $F_{1,43} = 3.82$, $p = 0.057$). It was affected by rainfall (inverse transformed) (GLM, $F_{1,43} = 9.69$, $p < 0.01$) and wind speed (GLM, $F_{1,43} = 9.79$, $p < 0.01$) with shorter night roosting bouts associated with increased rainfall and stronger winds. Interaction terms were removed during model simplification.

4.5 *Discussion*

A large number of roosts in addition to the maternity roost were located as a result of the radio-tracking and within the three contrasting landscapes the density of roosts was broadly similar. The bats showed loyalty to one or more roosts found in buildings and displayed only occasional; probably opportunistic use of trees. The use of buildings explains the strong association of roosts with settlements. Interestingly distribution of roosts around the maternity roost was non-uniform in the lowland and upland areas, implying a restricted or clumped distribution, but uniform for the high quality landscape. The uniform distribution in this locality could help explain why this landscape supports over four times the estimated foraging density of bats than the lowland and upland areas (refer to Chapter 3).

Roost switching is common in insectivorous bats, particularly in species that roost in trees, for example *Myotis californicus* (Brigham et al. 1997), *Chalinolobus tuberculatus* (O'Donnell and Sedgeley 1999), *Eptesicus fuscus* (Willis and Brigham 2004), *Myotis daubentonii* (Lučan et al. 2005), *Barbastella barbastellus* (Russo et al. 2004) but is less frequent in species that roost in more stable and less abundant sites, such as buildings and caves (Lewis 1995), for example *Plecotus auritus* (Entwistle et al. 2000), *Eptesicus serotinus* (Harbusch and Racey 2006). In concurrence with this pattern, roost switching by the colony as a whole was not observed in this study although alternative day roosts were frequently used by individual *R. hipposideros*. At least one third of the tracked bats were recorded day roosting away from the maternity roost on one or more occasions. A maximum of three roosts were used and roosts were on average a similar distance

from the maternity roost across the contrasting landscapes (mean range 1.15–1.26 km).

Roost switching may reflect the avoidance of predation, disturbance, or parasitism, selection of optimal microclimate and minimisation of distance to feeding sites (Kunz 1982, Lewis 1995, 1996, O'Donnell and Sedgeley 1999, Kunz and Lumsden 2003, Lausen and Barclay 2003, Willis and Brigham 2004). Some bats utilised alternative day roosts following tagging then subsequently returned to the maternity roost suggesting that the disturbance may have resulted in a temporary change in behaviour. However use of alternative roosts was otherwise thereafter sporadic suggesting other factors were also having an effect. Seckerdieck *et al.* (2005) found that *R. hipposideros* recurrently changed roosting sites during the reproductive season and suggest the opportunity to choose between different roosts appears to be energetically beneficial for breeding. They determined ambient temperature at night to be the most decisive factor for roost choice. In contrast, in the current study mean weather conditions during the previous night and at dawn were not found to affect choice of roosting location, although field data imply that heavy rainfall prior to dawn occasionally restricted movement of individuals back to the maternity roost.

Use of alternative roosts did vary according to reproductive status with lactating females and juveniles least likely to use alternative day roosts, suggesting greater philopatry at this time. Roost switching was most frequently recorded in females during early pregnancy and post-lactation and it is possible that this coincides with increased use of daily torpor to reduce energy demand. In *Plecotus auritus* Speakman and Racey (1987) found that daily torpor was used in early pregnancy before they became continuously endothermic in late pregnancy. In *Myotis daubentonii* (Dietz and Kalko 2006) torpor was used to the greatest extent during post-lactation. Ambient temperatures within the various roosts were not recorded as part of this study so it is not possible to confirm whether bats were selecting roosts according to their thermoregulatory costs and this aspect would warrant further study.

A high proportion of the day roosts (69 %) were also used as night roosts by the same individual. Night roosts were significantly closer to the core foraging areas than the maternity roost supporting the hypothesis that roost switching allows minimisation of distance to feeding sites. It is noteworthy that use of day roosts was more frequent when bats were less sessile and philopatric to the maternity roost suggesting the importance of alternative day roosts outside the key breeding season (late pregnancy and lactation).

Over three-quarters of the tagged bats night roosted away from the maternity roost, . typically in buildings. Occasional use of trees was recorded but this was believed to be opportunistic as use was not repeated. Night roosting was restricted to the maternity roost in only 19 % of the bats sampled. These were adult females during late pregnancy and lactation, and juveniles, although use of alternative night roosts was recorded in each group. A maximum of five different night roosts were used but there was no difference in number used according to landscape or reproductive status. Night roosts were on average 1.3–2.4 km from the maternity roost and, as stated earlier, were significantly nearer to core home range areas, with 56–64 % actually contained within core nuclei.

Feeding habitat has been shown to be important for selection of maternity roosts in buildings, for example in *Plecotus auritus* (Entwistle et al. 1997), *Pipistrellus* sp. (Oakeley and Jones 1998) and *R. hipposideros* (Reiter 2004a). Therefore it is likely that feeding habitat is also important for selection of night roosts. Conversely, however, I suggest that given the proximity of night roosts to the core areas, feeding habitat may equally be constrained by availability of night roosts. Number of night roosts was significantly correlated with home range parameters (home range, core area and range span). Therefore it may be postulated that reduction in availability of night roosts could result in corresponding reduction in home range. Availability of suitable maternity roosts may represent a primary constraint on the population size and distribution of different bat species (Humphrey 1975) and further work is required to determine if this is also the case with night roosts for *R. hipposideros*.

As previously illustrated in Chapter 3 (Section 3.4), the bats showed multimodal phases of activity throughout the breeding season with significantly more bouts occurring during post-lactation. Bontadina *et al.* (2002) also report a multimodal pattern, with two to four foraging bouts (mean 2.4 of 13 nights complete data). The multimodal pattern is unusual as insectivorous bats characteristically follow a bimodal pattern of activity (Erkert 1982), whereby a peak in activity is recorded following emergence from the roost at dusk, with a second smaller peak at the end of the night before dawn.

Variation in overnight activity patterns does occur in relation to physiological changes. For example, Swift (1980) and Maier (1992) found that *Pipistrellus* sp. exhibited a unimodal pattern during pregnancy, becoming bimodal during lactation, and then unimodal once again following weaning. More recent work on *P. pygmaeus* concurred with these findings (Davidson-Watts and Jones 2006). In *Nyctalus leisleri* activity is either unimodal or bimodal (Waters et al. 1999). In the Rhinolophidae a bimodal pattern has been observed in *R. ferrumequinum* (Duvergé and Jones 1994) and a typically unimodal pattern in *R. eurayle* (Aihartza et al. 2003).

Several hypotheses have been used to explain night roosting in bats, including thermoregulation (Anthony et al. 1981), exchange of information (Wilkinson 1992), a reduction in prey availability (Anthony et al. 1981) and digestion of food (Barclay 1982). Anthony *et al.* (1981) observed that night roosting decreased with increasing temperature and postulated night roosts are used for thermoregulation. However, I found that warmer temperatures were associated with a greater proportion of the night spent roosting. In addition windier conditions or increased rainfall resulted in bats foraging for longer. Therefore it seems unlikely that night roosts serve primarily in a thermoregulatory capacity for *R. hipposideros*. In terms of the second hypothesis, as internal checks on night-roosts were avoided in the study to avoid disturbance and disruption of activity patterns it is not possible to comment on the potential social function of these roosts. However, roosts are likely to be communal, as they were used by more than one individual from the same colony during successive tracking sessions. When exploring kin-biased behaviour in *R. ferrumequinum*, Rossiter (2002) often found that female bats and

their adult daughters shared night roosts, sometimes over several years, and no cases were recorded of non-relatives using the same night roost. Night roosts may therefore be important centres for information transfer among relatives, and this should be considered in conservation.

Reduction of prey availability explains unimodal or bimodal behaviour as peaks of activity coincide with overnight peaks in insect numbers at dusk, and to a lesser extent, dawn (Taylor 1963). I have previously argued that gleaning is not the principal foraging stategy with the majority of prey caught on the wing during aerial hawking and that dusk and dawn are important foraging times for *R. hipposideros* (refer to Chapters 2 and 3). However moths and non-volant prey are also present in the diet. Moths are active all night, with a peak activity in moths occurring around midnight (Rydell et al. 1996), and non-flying prey are also available all night. The broad diet of the species may therefore allow them to feed throughout the night, for example feeding predominantly on swarming insects at dusk and dawn, and mainly on moths and non-volant prey and insects resting on vegetation during the intervening period, hence resulting in multimodal activity. As such a reduction in prey availability is unlikely to explain use of night roosts in this species.

Given periodic feeding throughout the night, and the presence of faecal pellets within night roosts, it does seem likely that night roosts are used for digestion of food. I have shown that night roosts are in close proximity to the core foraging areas and their use allows minimisation of distance to feeding sites. I suggest that minimisation of distance to feeding sites may be the primary function of these night roosts, being used for resting and digestion between foraging bouts, with a secondary use for communal behaviour, and possibly thermoregulation. As such I postulate they form an integral part of the core foraging areas.

Implications for conservation and future research

The multimodal nature of activity and frequent use of night roosts, and alternative day roosts, is an important aspect of *R. hipposideros* behaviour. It needs to be considered carefully when designing management strategies to conserve the

species. The study has highlighted the importance of rural settlements for *R. hipposideros* but the fact that day and night roosts are typically in buildings often leads to conflict. Many of the barns and outbuildings utilised are of period construction and the potential for conversion to dwellings is high. Briggs (2004) demonstrated the lack of success of mitigation during barn conversions. In a survey of 36 barn units previously supporting vespertilionid bat roosts that had undergone conversion, only 22 % of the units were used by bats post development, despite a further 42 % still having potential for use.

The effect of loss of roosts on bat populations is poorly understood and difficult to study (Mitchell-Jones 2004) but has long been recognised as a significant threat (Hutson 1993). The impact of loss of night roosts is currently regarded as low, although this is a general guide only and does not take into account species differences (Mitchell-Jones 2004). However given the loyalty of *R. hipposideros* to these roosts and the potential for them to form an integral part of the core foraging areas and for kin-related use, then the impact is likely to be much greater, particularly to the individual/s concerned. Although loss of individual roosts may not necessarily affect the viability of the maternity colony, impacts could well be cumulative.

The reasons behind use of night and alternative day roosts for this species need to be more fully understood and further research is required. For example, monitoring ambient temperature levels and use of infra-red and video-monitoring to monitor activity levels would help to explore thermoregulatory capacity and other aspects of use. The degree of selectivity of sites should be explored (Schofield 1996, Entwistle et al. 1997) to enable night roosts to be fully characterised. Finally, an experimental approach may be required to assess the effect of loss of night roost on the bats' behaviour and range parameters, such as core foraging area and overall home range. The temporary removal of a night roost during a radio-tracking session may be one method but use of such an approach in a vulnerable species such as *R. hipposideros* would need careful consideration and may be deemed unacceptable.

CHAPTER FIVE

HABITAT AND LANDSCAPE USE BY *R. HIPPOSIDEROS*

5 Habitat and landscape use by *R. hipposideros*

5.1 *Summary*

I examined habitat use by *R. hipposideros* during the breeding season by using radio-telemetry in three counties of England and Wales. Habitat composition within home ranges was significantly different from the study area in the lowland and upland landscapes but not so for the high quality locality. Geographical variation in habitat selection existed. Broad-leaved woods, water, rural settlements and pasture fields with wooded edge or unmanaged hedges were the most utilised habitats. The results broadly agree with implications drawn from dietary analysis.

Overall, broad-leaved tree cover of 26–90 % was utilised more than available in the core foraging areas with continuous tree cover (91–100 %) least utilised. This pattern was also demonstrated when combining level of tree cover with habitat. Pasture fields with over 25 % associated tree cover and settlements with 1-10 % and 26-75 % associated tree cover were selected for above their availability. I postulate that tree cover, and not necessarily woodland *per se*, and edge habitats are of key importance for *R. hipposideros*. The estimated foraging density and overall colony sizes were reflected in both increased coverage of preferred habitats and increased edge. I suggest that level of tree cover and/or availability of edge habitats may be more closely correlated with the carrying capacity of a given area than extent of broad-leaved woods and this warrants further investigation.

Habitat occurrence within home ranges was significantly different from the study area throughout the breeding season in the lowland but only post-natal females selected habitats in core areas. This may relate to changes in energy requirements, with habitat selection corresponding with times of highest energy needs. There was no significant difference between habitat composition of home ranges of nulliparous females and juveniles and the study area, although this may be a consequence of small sample sizes. An expansion of home ranges and exploitation of different feeding areas occurred in juveniles.

5.2 *Introduction*

Habitat loss and fragmentation has been recognised as a prevailing cause of landscape change and is a major cause of declining biodiversity (Wilcox and Murphy 1985). In particular, forest loss and fragmentation has been one of the most important alterations to the global landscape (Hobbs and Saunders 1993). Habitat fragmentation involves 1) an overall loss of habitat; 2) a reduction in the size of the blocks of habitat; and 3) an increased isolation of habitats (Bennett 1999). Despite being mobile species, bats are highly susceptible to habitat fragmentation (Bright 1993, Walsh and Harris 1996a) and many species are declining across Britain and Europe (Stebbings 1988, Mitchell-Jones 1994-1995, Hutson et al. 2001). *R. hipposideros* has undergone a particularly dramatic decline and is now virtually extinct in large areas of north-west Europe (Ohlendorf 1997).

The most important and large-scale cause of habitat fragmentation is the expansion and intensification of land-use through intensive farming practices (Burgess and Sharpe 1981). Documented effects include the loss of hedges and ponds (Entwistle et al. 2001) and an increase in average field sizes as hedgerows have been removed (Westmacott and Worthington 1997). In particular, woodland (including coniferous) once covered up to 90% of the land area in Britain (Rackham 1986), but has now been reduced to 12% (Haines-Young et al. 2000). The degree of agricultural intensification varies across the country. For example arable farming now dominates in the east and pastoral farming in the west (Macdonald and Tattersall 2001), with pockets of more traditionally managed areas existing only as isolated patches. More than 76 % of the land in Britain is used for agriculture (Robinson and Sutherland 2002) and farmland is the primary habitat for many species, for example skylark *Alauda arvensis*, tree sparrow *Passer montanus*, linnet *Carduelis cannabina*, starling *Sturnus vulgaris* (Siriwardena et al. 1998, Krebs et al. 1999), and brown hare *Lepus europaeus* (Harris et al. 1995).

Within Britain *R. hipposideros* is distributed across Wales and south-west England (Richardson 2000) with populations occurring predominantly within the lowland agricultural landscape, as well as areas of upland, such as Dartmoor and Snowdonia National Parks. Exceptional populations that are significant in both a

national and European context are found within the Lower Wye Valley (Monmouthshire and Gloucestershire) and Royal Forest of Dean (Gloucestershire) (Wye Valley and Forest of Dean Bat Sites Special Area of Conservation), which I have classified as a high quality landscape for the species (refer to Chapter 2, section 2.3.1 for details). Traditional pastoral farming predominates, with characteristic areas of small flower-rich fields, unmanaged hedgerows, tree belts and small woodlands. Broad-leaved deciduous woodland is a key foraging habitat for *R. hipposideros* (Bontadina et al. 2002) and as detailed in Chapter 2 (section 2.3.1) the amount of broad-leaved deciduous woodland cover is *c.*20% higher than the national average. Therefore the presence of *R. hipposideros* within both intensively managed and traditionally managed lowland, together with a marginal upland landscape, represents a valuable opportunity to study geographical differences in habitat use and to consider whether habitat fragmentation is a contributing factor to any perceived differences. I hypothesise that habitat use will vary among landscape types, with the species predominantly utilising broad-leaved woodland in the high quality landscape but a greater range of habitats in the lowland and upland, given the paucity of woodland cover in these areas.

I examined the habitat and landscape use of *R. hipposideros* within three distinct landscape types in Britain, using a large-scale radio-tracking study, to determine whether spatial and seasonal variation exists.

The specific aims of this chapter are:

1. To determine whether habitat occurrence within individual home ranges was significantly different from the study area and, if so, to determine whether the bats selected habitats or used them according to availability.
2. To test the hypothesis that habitat use varies across different landscape types in Britain.
3. To determine any changes in habitat use according to reproductive status.
4. To describe any similarities between my study and previous limited research into habitat preferences of *R. hipposideros.*

5. To investigate the link between habitat use and diet (Chapter 2) and foraging behaviour (Chapter 3).

5.3 *Methods*

5.3.1 *Study colonies and land use mapping*

The radio-tracking study of *R. hipposideros* was conducted during the summers of 2003, 2004 and 2005 during early to late May (early pregnancy), late May to early June (late pregnancy), late July to mid-August (lactation) and late August to mid-September (post-lactation). Bats were sampled from three maternity roosts representing the key landscape types that characterise the distribution of *R. hipposideros* in Britain: lowland (Roost A, North Somerset), a high quality landscape (Roost B, Wye Valley, Gloucestershire and Monmouthshire) and upland (Roost C, Powys). Bats were radio-tracked from Lowland A in 2003, High Quality B in 2004 and Upland C in 2005. To allow comparison between data and the assessment of habitat use within a lowland landscape more fully, Lowland A was studied in each of 2003, 2004 and 2005. Such an approach would hopefully control for any differences that might occur across years within the same landscape type.

The 'study area' is defined as a maximum range circle (MRC) centred on the roost site, containing all of the fixes of the radio-tracked bats from the colony. Consequently the 'study area' considered for habitat selection analyses varied according to the bats behaviour in different landscapes. Human disturbance factors occurring also varied according to landscape type but broadly included agriculture (pasture and arable), conifer plantations and urbanisation and settlements.

Base maps (Ordnance Survey Land-Line.Plus, multi-scale) were obtained from Digimap (© Crown Copyright Ordnance Survey, EDINA Digimap/JISC) and converted for use in the GIS software ArcView GIS 3.2 (Environmental Systems Research Institute, Inc.) with Map Manager (Environmental Systems Research Institute, Inc.). Land use maps (vector format) were then generated with ArcView using information gained from Phase 1 habitat surveys (Anon 1993) I undertook

during the field seasons, together with aerial photograph data (supplied by Countryside Council for Wales, Gwynedd; Natural England, Peterborough), supplemented by information supplied by local Biological Records Centres where access permission was denied. Three land-use maps were created for the lowland locality to reflect changes in habitat availability during the three-year tracking period at this site.

The following 12 habitat types were recognised and broadly follow the habitat definitions in the Phase 1 habitat survey guidelines (Anon 1993):

1. Broad-leaved woodland. Semi-natural and plantations of broad-leaved species with 10 % or less conifer in the canopy.
2. Coniferous plantation. 10 % or less broad-leaved species in the canopy.
3. Mixed woodland. 10-90 % of either broad-leaved or conifer in the canopy.
4. Scrub. Dense or semi-continuous stands of shrub species less than 3 m tall.
5. Parkland and orchards. Open sites with scattered trees, includes recently planted and established orchards.
6. Improved pasture. Permanent pasture or re-seeded leys with low species diversity that have been subjected to high degree of agricultural improvement.
7. Semi-natural grassland. Permanent pasture (unimproved or semi-improved) with a higher species diversity than improved pasture.
8. Arable. Cropland and horticultural land subject to ploughing and disturbance. Typical crops include maize *Zea mays* and wheat *Triticum* spp.
9. Amenity. Intensively managed and regularly mown grasslands such as playing fields and golf course fairways.
10. Riparian. Areas of open water (ponds, lakes, rivers, streams) and associated features such as marsh.
11. Bracken/heath. Areas dominated by bracken *Pteridium aquilinum* or ericoids or dwarf gorse species *Ulex* spp.
12. Settlements. Built-up areas with associated gardens and infrastructure. Includes roads and individual scattered properties and villages/towns.

In addition, areas of improved pasture, semi-natural grassland and arable were subdivided to include details of hedgerows. Hedges were categorised as unmanaged if they were 3 m or more in height with a continuous or semi-continuous canopy structure. Managed hedges were defined as less than 3 m in height, having been flailed or laid. Hedgerow categories did not take species composition into account. Fields within farmland categories 6, 7 and 8 were subdivided into those with tall, unmanaged hedgerows or woodland on one or more of their boundaries (subcategory +) and those with only managed or largely defunct hedges, fences or stone walls. Fields within farmland categories 6, 7 and 8 were also divided into those of organic status (Lampkin 1998) compared with those being conventionally farmed.

To investigate the effect of broad-leaved tree cover further, the area used by all of the tracked bats in the lowland landscape was subdivided into 100 m grid squares (using the 6-figure Ordnance Survey National Grid Reference System). The grid cell size reflects the accuracy of the fixes obtained by the radio-tracking (Harris et al. 1990). For each grid square an estimate of broad-leaved tree cover was made using recent aerial photographs (supplied by Natural England, O.S. licence no. 100046223) on the following scale: 1 = 0 %, 2 = 1-4 %, 3 = 5–10 %, 4 = 11-25 %, 5 = 26-50%, 6 = 51-75 %, 7 = 76-90 %, 8 = 91-100 % tree cover.

To also take habitat type into account in addition to level of broad-leaved tree cover, pasture, arable and settlement habitat types were subdivided into sub-categories based on the above scales of tree cover. In the subsequent analysis, due to restrictions on number of habitat types allowed, it was necessary to combine sub-categories 2 and 3 (i.e. 1-10 %) and 7 and 8 (76-100 %).

5.3.2 *Data collection*

For details of capture and tagging methods, and radio-tracking equipment and data collection refer to Section 3.3.1 and 3.3.2, Chapter 3.

5.3.3 *Data analysis*

Habitat use

The determined or estimated bat locations were displayed with ArcView GIS 3.2 (Environmental Systems Research Institute, Inc.). Home-range analyses were undertaken using the Ranges 6 v1.2 (Kenward et al. 2003) and a pre-release version of Ranges 7 v1.0 analysis system (South and Kenward 2006) (Anatrack Ltd., Wareham, UK). Home ranges were calculated as 100 % minimum convex polygons (MCPs) (Mohr 1947) of all locations to allow comparison with other studies as recommended by Harris *et al.* (1990). I then used cluster analysis (Kenward 1987, 2001) to create 85 % cluster cores to assess 'active core home range' using active fixes only. For full details of methods used refer to Section 3.3.3, Chapter 3. Home ranges were then overlaid onto the habitat maps generated for each study area and two different analyses comparing habitat use with habitat availability were performed:

1. On a broad scale, percent habitat composition within each bat's MCP was compared with that of the study area (based on the MRC) to determine whether habitat occurrence within individual home ranges differed significantly from that of the study area.
2. On a finer scale, percent habitat composition within each bat's core home range was compared with that of the bat's MCP to investigate whether the bats selected habitats or used them according to availability.

These steps were repeated using the tree cover map generated for the lowland landscape, with the colony MCP (i.e. MCP of fixes from all tracked bats) replacing the MRC in step 1.

Finally, to assess whether the bats selected habitats or used them according to availability for commuting, the comparison of percentage habitat composition within 50 m buffers around an individual's commuting fixes was compared with that of the corresponding MCP.

All comparisons were carried out using compositional analysis. In this method, log-ratio differences between proportions of used and available habitats are entered for analysis, and each bat represents a sample unit. Compositional analysis was performed with Compositional Analysis Excel tool 3.1 written by Dr. P Smith (University of Aberdeen) according to the methods of Aebischer *et al.* (1993).

Boundaries of pastoral and arable fields were digitised in the land use maps. As the lowland locality was radio-tracked over three years the land use map from 2003 was used. The mean field area was calculated for all fields wholly contained within a 2 km radius around each maternity roost, the rationale being that 2 km was the mean maximum distance travelled by the bats in each locality (refer to Section 3.4, Chapter 3).

Landscape use

Home range analysis describes the spatial extent of animal movements but generally provides limited insight into spatial dispersion (Hagen et al. 2001). To further characterize the dispersion patterns of the radio-tracked bats relative to locality I undertook a multiscale analysis of the radio-tracking data based on fractal geometry as advocated by Hagen *et al.* (2001). The fractal dimension, D, provides valuable information on how a population uses the landscape (With et al. 1999) and gives a scale-invariant measure of spatial contagion, i.e. dispersion of fixes. The fractal dimension for the utilisation distribution (point pattern of fix locations) of all bats tracked per locality was estimated using the box counting method (Gautestad and Mysterud 1993). A large sample size ($n > 500$) is required to avoid the dilution effect (Hagen et al. 2001) so all fixes from each locality were used (lowland $n = 2124$, high quality $n = 572$, upland $n = 678$). A grid of non-overlapping boxes was superimposed over the point pattern in ArcView and number N of boxes occupied at box size of side length, $s = 100$ m (minimum tracking resolution), 200 m, 300m, 400m, 500m, 800m, 1000m and 2000m was determined. The fractal dimension was calculated from the slope of regression line between log (N) and log (s). The point pattern is fractal if the slope is linear i.e. independent of scale. If D = 2, then an individual behaves randomly, eventually

visiting all areas of the home range. If $D < 2$, then the point pattern is contagious, becoming increasingly more clumped as D reduces.

Landscape analyses were undertaken using FRAGSTATS version 3.3 build 4, a spatial pattern analysis program for categorical maps (McGarigal et al. 2002). It quantifies the extent and spatial configuration of patches within a landscape by computing metrics. Vector maps were converted to grids using ArcView's Spatial Analyst extension (Environmental Systems Research Institute, Inc.). The scale and extent of the grids define the landscape within FRAGSTATS and computed metrics are meaningful only if the measured pattern of the landscape is functionally meaningful for the organism under consideration (McGarigal et al. 2002). The smallest scale at which an organism responds to patch structure is its 'grain' (Kotliar and Wiens 1990). I set the grain (equivalent to grid cell size) as 10 m to corresponds to both the maximum resolution of my tracking data and accuracy of original vector land-use maps. I initially set the extent, which defines the landscape boundary, to be the MRC. However although this does reflect the area used by the tracked bats in each locality, McGarigal *et al.* (2002) state that caution is required when comparing the value of metrics computed for landscapes that have been defined and scaled differently. Therefore to overcome this I also defined the landscape boundary as the 2 km radius around the maternity roost. Patches within the landscape were defined as habitat types. To enable comparisons between sites, 10 habitat categories which were present in each landscape were used: broad-leaved woodland (including scrub and parkland), coniferous woodland, mixed woodland, pasture+ (improved and semi-natural grassland, including amenity, with tall hedgerows/adjacent woodland), pasture (improved and semi-natural grassland lacking tall hedgerows/adjacent woodland), arable+, arable, water, bracken/heath and settlements.

Class-level and landscape-level metrics were computed. As habitat analysis was undertaken using the vector maps, patch-level metrics were omitted from the analysis. Class metrics quantify the amount and spatial configuration of each habitat type and thus provide a means to quantify the extent and fragmentation of each habitat type in the landscape. Landscape metrics represent the spatial pattern of the entire landscape mosaic and give an index of landscape heterogeneity

(McGarigal et al. 2002). I calculated two metrics, one at class-level (1) and one at landscape-level (2):

1. degree of contagion (CLUMPY), a measure of the extent to which cells of similar habitat are spatially aggregated.
2. landscape shape index (LSI), which provides a standardised measure of total edge or edge density that adjusts for the size of the landscape.

Finally, General Linear Modelling (GLM) was used to analyse whether field sizes and the class-level metric varied according to habitat type and/or locality, together with Tukey's post-hoc multiple comparisons. For full details of the GLM methods, including the model simplification process and assumptions of the GLM, refer to Section 3.3.3, Chapter 3. The analysis was carried out using Minitab version 13.32 for Windows with a critical value of $\alpha = 0.05$.

5.4 *Results*

During the three-year study (2003-5) data were obtained from 54 bats fitted with radio-transmitters (refer to Table 3.1, Chapter 3, for sampling effort). 36 bats were radio-tracked from the lowland locality: 6 adult females in early pregnancy, 6 adult females in late pregnancy, 6 adult females during lactation, 6 adult females during post-lactation, 6 nulliparous females and 6 juveniles (2 females, 4 males). A further 18 bats were tracked in the high quality and upland landscapes (3 adult females in late pregnancy, 3 adult females during lactation and 3 adult females during post-lactation at each locality).

5.4.1 *Habitat use*

Figure 5.1 gives the habitat composition of the 2 km radius around the three maternity roosts that were used in the radio-tracking study. The high quality landscape featured a higher percent cover of broad-leaved woodland and pasture+ fields (improved and semi-natural grassland, including amenity, with adjacent tall hedgerows/woodland). In the upland locality bracken/heath comprised over 50 % of the landscape, with only a small proportion of settlements in comparison with the other two localities.

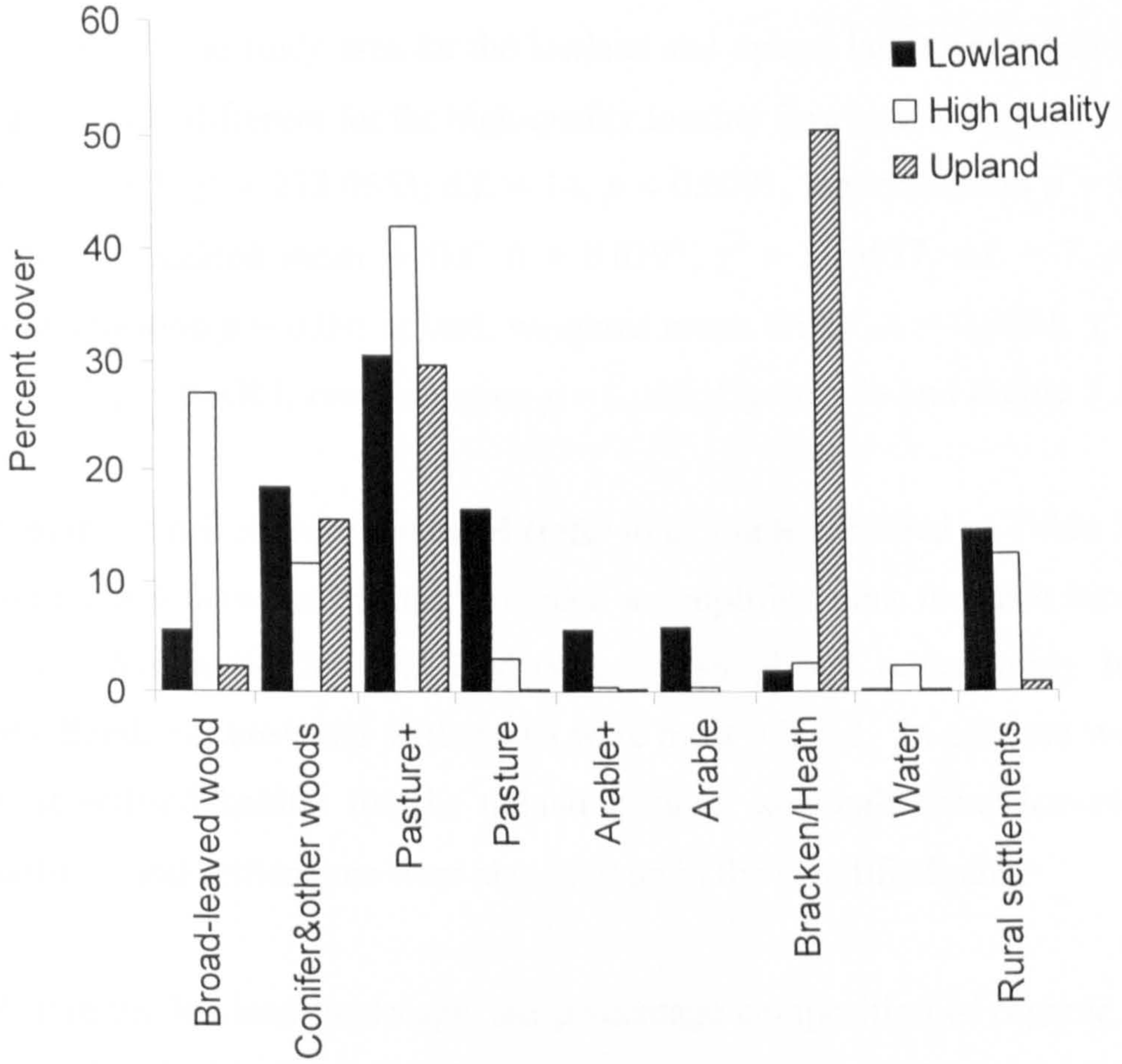

Figure 5.1. Habitat composition of the 2 km radius around the *Rhinolophus hipposideros* maternity roosts within three contrasting landscapes that were used in the radio-tracking study. +, fields with tall, unmanaged hedgerows or woodland on one or more of their boundaries compared with those with only managed or largely defunct hedges, fences or stone walls.

Percentage habitat composition of individual MCP areas differed significantly from that of the study area for the lowland and upland landscape types but was not significantly different for the high-quality locality (lowland: weighted mean Wilks' $\Lambda = 0.0005$, $\chi^2 = 273.0553$, d.f. = 14, $p < 0.0001$, randomisation $p = 0.001$; high quality: weighted mean Wilks' $\Lambda = 0.0297$, $\chi^2 = 31.6557$, d.f. = 7, $p < 0.0001$, randomisation $p = 0.09$; upland: weighted mean Wilks' $\Lambda = 0.0001$, $\chi^2 = 88.3764$, d.f. = 7, $p < 0.0001$, randomisation $p = 0.005$; Figure 5.2a and Figure 5.3a).

Ranking matrices were produced (refer to example provided in Table 5.1) and the comparison between habitats provided a simplified rank for each locality (Table 5.2). Within the lowland landscape the simplified ranks imply broad-leaved woodland, pasture+ and settlements were most utilised. In contrast water was the most utilised habitat for the upland locality, although broad-leaved woodland, pasture+ and settlements were also high up in the simplified rank.

Within the lowland landscape, the percentage composition of organic farmland in individual MCPs did not differ significantly from that of the study area (weighted mean Wilks' $\Lambda = 0.9900$, $\chi^2 = 0.3631$, d.f. = 1, $p > 0.05$, randomisation $p = 0.522$).

At the lowland locality percentage habitat composition of individual MCP areas differed significantly from that of the study area in both pre- and post-parturition for adult female bats (pre-parturition: weighted mean Wilks' $\Lambda = 0.0002$, $\chi^2 = 105.5821$, d.f. = 10, $p < 0.0001$, randomisation $p = 0.003$; post-parturition: weighted mean Wilks' $\Lambda = 0.0000$, $\chi^2 = 151.3837$, d.f. = 10, $p < 0.0001$, randomisation $p = 0.002$; Table 5.2).

In contrast there was no significant difference between habitat composition of individual MCP areas of nulliparous females and juveniles and the study area (nulliparous females: weighted mean Wilks' $\Lambda = 0.2495$, $\chi^2 = 8.3308$, d.f. = 4, $p = 0.0802$, randomisation $p = 0.4880$; juveniles: weighted mean Wilks' $\Lambda = 0.0882$, $\chi^2 = 14.5703$, d.f. = 4, $p < 0.01$, randomisation $p = 0.149$).

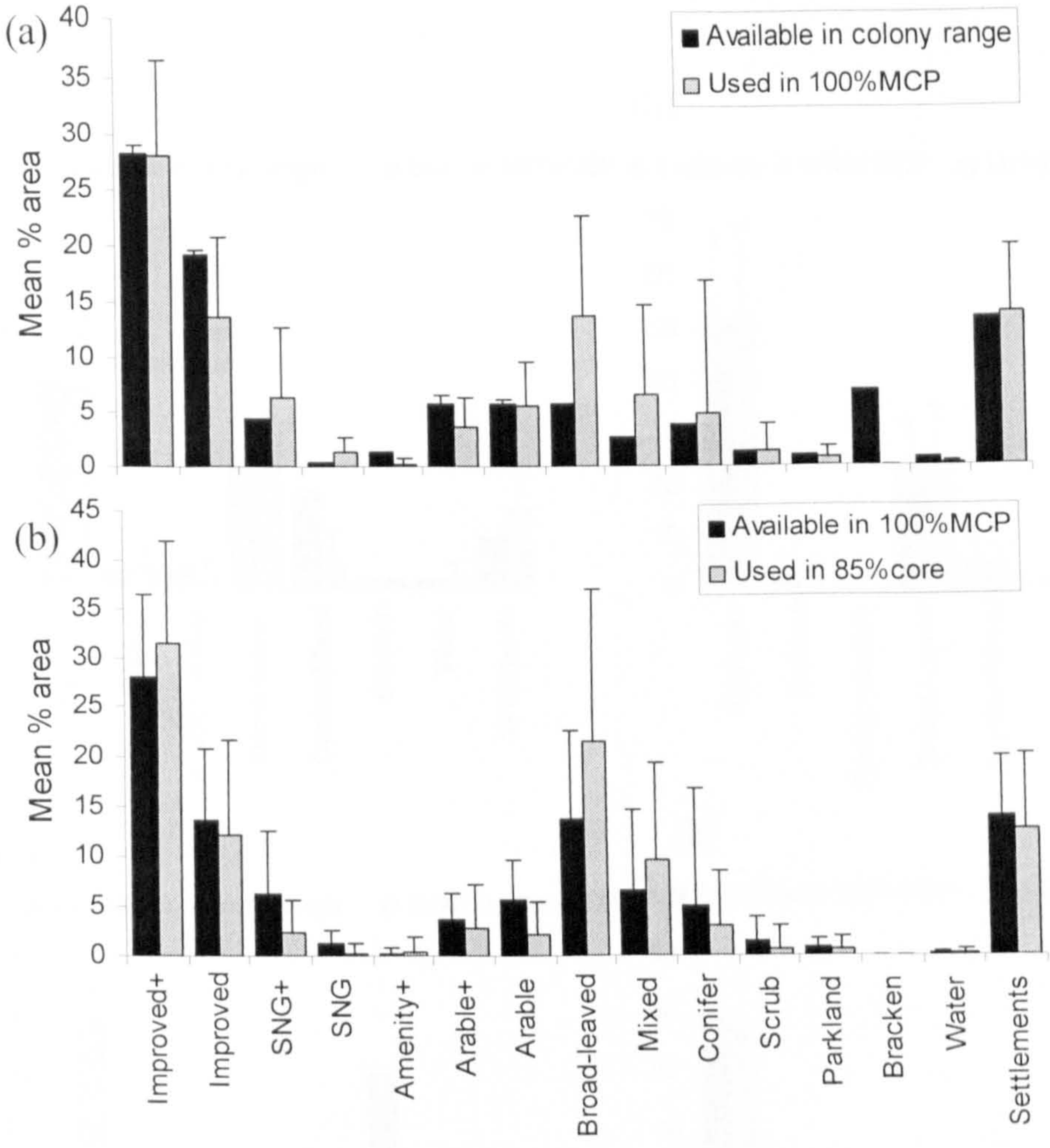

Figure 5.2. Habitat selection by *Rhinolophus hipposideros*: comparisons of habitat available *vs*. habitat used (mean percentage area ±SD) in the lowland landscapes. (a) Selection of home ranges: comparison of the habitat available in the colony range (defined by the maximum range circle) with the home range (minimum convex polygon (MCP)). (b) Selection of core foraging areas: comparison of the individual MCP with core foraging areas (defined by the 85% core of active fixes). SNG, semi-natural grassland. +, fields with tall, unmanaged hedgerows or woodland on one or more of their boundaries compared with those with only managed or largely defunct hedges, fences or stone walls.

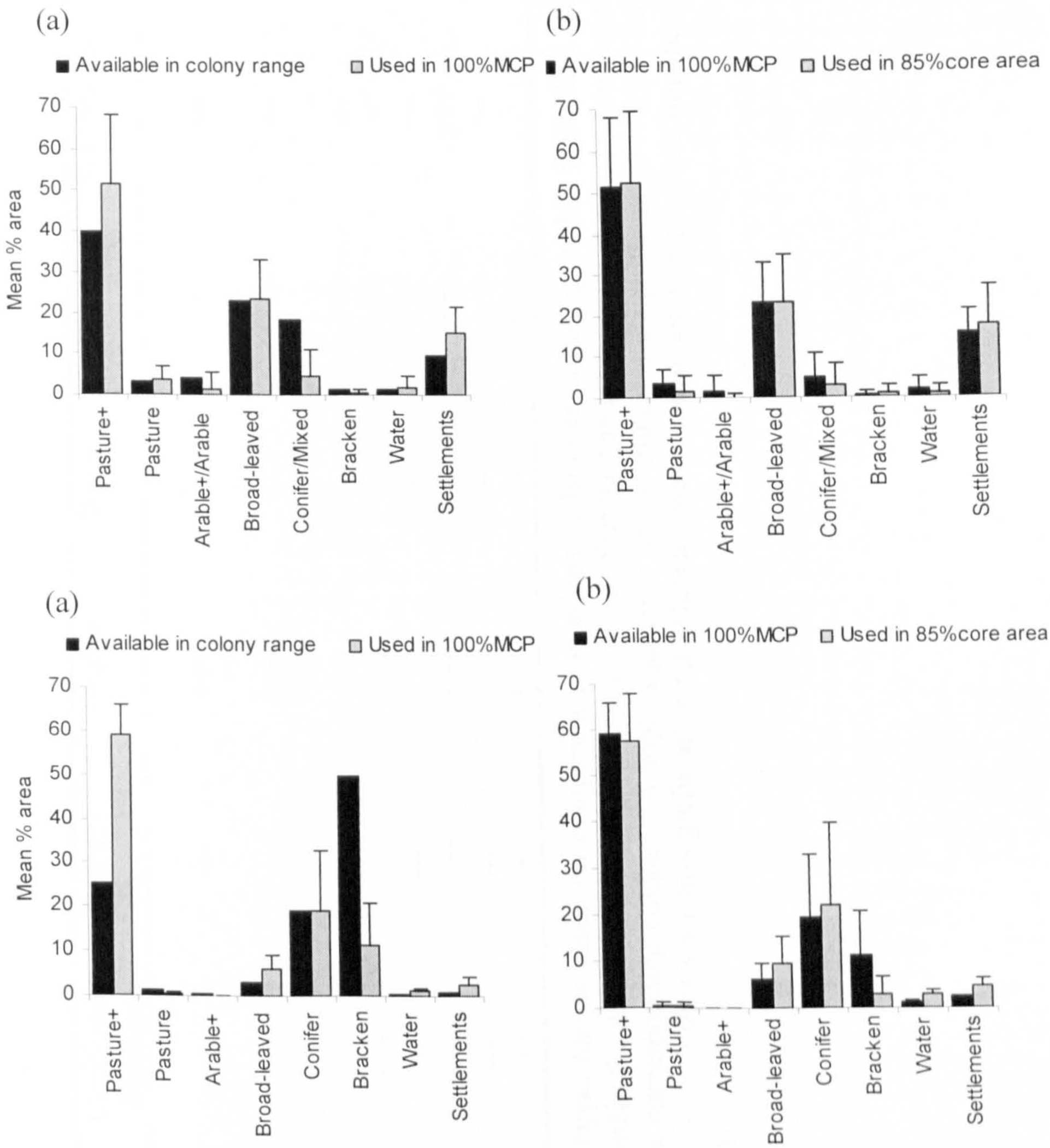

Figure 5.3a&b. Habitat selection by *Rhinolophus hipposideros*: comparisons of habitat available *vs* habitat used (mean percentage area ±SD) in the high quality (top) and upland landscapes (bottom). (a) Selection of home ranges: comparison of the habitat available in the colony range (defined by the maximum range circle) with the home range (minimum convex polygon (MCP)). (b) Selection of core foraging areas: comparison of the individual MCP with core foraging areas (defined by the 85% core of active fixes). +, fields with tall, unmanaged hedgerows or woodland on one or more of their boundaries compared with those with only managed or largely defunct hedges, fences or stone walls.

	Bracken/ heath	Broad-leaved woodland	Coniferous woodland	Pasture+	Arable+	Water	Pasture	Settlements	Rank
Bracken/ heath		---	---	---	+++	---	+	---	2
Broad-leaved woodland	+++		+	-	+++	---	+++	---	4
Coniferous woodland	+++	-		---	+++	---	+++	---	3
Pasture+	+++	+	+++		+++	---	+++	-	5
Arable+	---	---	---	---		---	-	---	0
Water	+++	+++	+++	+++	+++		+++	+++	7
Pasture	-	---	---	---	+	---		---	1
Settlements	+++	+++	+++	+	+++	---	+++		6

Table 5.1. Ranking matrix for *Rhinolophus hipposideros* based on comparing proportions of habitats occurring within individual minimum convex polygons and those in the study area within the upland locality. The signs show whether the habitat placed in the corresponding row was more (+) or less (-) important than that in the corresponding column. A triple sign (+++ or ---) indicates a significant ($p < 0.05$) difference between the two habitat categories. One sign (+ or -) shows a non-significant trend. Habitats were ranked according to their importance from zero (least important) to seven (most important).

Analysis	*n*	MCP *vs.* study area		Active core *vs.* MCP	
		p	Habitat ranking	*p*	Habitat ranking
Pre-parturition	12	0.003	Broad-leaved > Mixed > Settlements > Pasture+ > Arable > Scrub/Parkland > Conifer > Pasture > Arable+ >>> Water >>> Bracken/Heath	NS	
Post-parturition	12	0.002	Broad-leaved > Settlements > Mixed > Pasture+ > Arable > Arable+ > Pasture > Scrub/Parkland > Conifer > Water >>> Bracken/Heath	0.006	Broad-leaved >>> Pasture+ > Pasture = Mixed > Water = Settlements > Conifer > Scrub/Parkland > Arable+ > Arable
Nulliparous	6	NS		NS	
Juvenile	6	NS		NS	
Overall	36	0.001	Broad-leaved > Mixed > Improved+ > Settlements > SNG > Arable > Improved > Arable+ > Parkland > Conifer > SNG+ > Water > Scrub >>> Amenity >>> Bracken/Heath	NS	

Table 5.2a. Compositional analysis results on habitat selection in *Rhinolophus hipposideros* within the lowland locality based on comparing proportions of habitat occurring within individual minimum convex polygons (MCP) and those in the study area, and comparing habitats occurring within individual active core areas and those in the corresponding MCP. When analysing differences according to reproductive status, the small sample sizes restricts number of habitat types so habitats were combined as follows: broad-leaved = broad-leaved woodland, parkland, scrub; pasture = improved, semi-natural grassland (SNG); pasture+ = improved+, SNG+, amenity. + = fields featuring an unmanaged hedgerow (3 m or more in height with a canopy structure) or woodland type along one or more boundary.

Locality	Analysis	*n*	MCP *vs.* study area		Active core *vs.* MCP	
			p	Habitat ranking	*p*	Habitat ranking
High quality	Overall	9	NS		NS	
Upland	Overall	9	0.005	Water >>> Settlements > Pasture+ > Broad-leaved > Conifer >>> Bracken/Heath > Pasture > Arable+	0.037	Water >>> Settlements > Broad-leaved > Conifer > Pasture+ >>> Bracken/Heath > Pasture

Table 5.2b. Compositional analysis results on habitat selection in *Rhinolophus hipposideros* within the high quality and upland localities based on comparing proportions of habitat occurring within individual minimum convex polygons (MCP) and those in the study area, and comparing habitats occurring within individual active core areas and those in the corresponding MCP.

Locality	Analysis	*n*	Individual MCP *vs.* colony MCP		Active core *vs.* MCP	
			p	Habitat ranking	*p*	Habitat ranking
Lowland	Percentage tree cover	36	0.001	76-90% >>> 51-75% > 1-4% > 26-50% > 5-10% > 91-100% > 11-25% > 0%	0.002	76-90% > 26-50% > 51-75% > 5-10% > 0% > 1-4% > 11-25% > 91-100%
Lowland	Rank tree cover & habitat type	36	0.001	Broad-leaved > Mixed > Pasture6 > Pasture7 >>> Pasture5 > Settlements2 > Pasture2 > Pasture1 > Pasture4 > Arable4 > Settlements6 > Arable2 > Arable1 > Settlements5 > Settlements4 > Parkland/Scrub > Settlements1 > Water > Conifer > Settlements7 > Arable7 > Arable5 > Arable6	NS	

Table 5.2c. Compositional analysis results on habitat selection in *Rhinolophus hipposideros* within the lowland locality based on comparing proportions of habitat occurring within individual minimum convex polygons (MCP) and those in the colony MCP, and comparing habitats occurring within individual active core areas and those in the corresponding MCPs. In the second analysis pasture, arable and settlement habitat types have been sub-divided into 6 subcategories, depending on the level of broad-leaved tree cover in the corresponding 100 m grid square: 1 = 0 %, 2 = 1-10 %, 4 = 11-25 %, 5 = 26-50%, 6 = 51-75 %, 7 = 76-100 % tree cover.

Locality	Analysis	*n*	50m buffers around commuting fixes *vs.* MCP	
			p	Habitat ranking
Lowland	Commuting	26	0.004	Settlements > Improved+ = Water > Broad-leaved = Amenity > Mixed > Improved > Conifer > SNG+ > Parkland > Arable > SNG > Arable+ > Scrub

Table 5.2d. Compositional analysis results on habitat selection in *Rhinolophus hipposideros* within the lowland locality based on comparing proportions of habitat occurring within 50 m buffers around an individual's commuting fixes and those in the corresponding minimum convex polygon (MCP).

On a finer scale, the percentage habitat composition within core areas (used) was significantly different from that of the individual MCPs (available) at the upland locality but not lowland nor high quality landscapes (lowland: weighted mean Wilks' $\Lambda = 0.0657$, $\chi^2 = 98.0105$, d.f. = 13, $p < 0.0001$, randomisation $p = 0.07$; high quality: weighted mean Wilks' $\Lambda = 0.0362$, $\chi^2 = 29.8600$, d.f. = 6, $p < 0.0001$, randomisation $p = 0.2430$; upland: weighted mean Wilks' $\Lambda = 0.0117$, $\chi^2 = 40.0022$, d.f. = 6, $p < 0.0001$, randomisation $p = 0.037$; Figure 5.2b and Figure 5.3b; Table 5.2). The simplified rank analysis implies that water was used significantly more than all other habitats except for pasture+ within the upland locality.

Percentage habitat composition within core areas (used) was significantly different from that of the individual MCPs (available) at the lowland locality post-parturition but was not significantly different pre-parturition (pre-parturition: weighted mean Wilks' $\Lambda = 0.2005$, $\chi^2 = 19.2825$, d.f. = 9, $p < 0.05$, randomisation $p = 0.5580$; post-parturition: weighted mean Wilks' $\Lambda = 0.0244$, $\chi^2 = 44.5696$, d.f. = 9, $p < 0.0001$, randomisation $p = 0.006$; Table 5.2). The simplified rank analysis implies that broad-leaved woodland was used significantly more than all other habitats except for mixed woodland.

The results imply broad-leaved tree cover may be of importance with broad-leaved and mixed woodland and pasture+ fields being higher up in the simplified rank. To investigate this further the broad-leaved tree cover maps for the lowland landscape were analysed. Percentage tree cover composition of individual MCP was significantly different from the colony MCP (weighted mean Wilks' $\Lambda = 0.1716$, $\chi^2 = 63.4539$, d.f. = 7, $p < 0.0001$, randomisation $p = 0.001$). Percentage tree cover composition within core areas (used) was also significantly different from individual MCPs (available) (weighted mean Wilks' $\Lambda = 0.5199$, $\chi^2 = 23.5456$, d.f. = 7, $p < 0.01$, randomisation $p = 0.002$). The simplified ranks are provided in Table 5.2c. The results imply that high percentage of broad-leaved tree cover, though not necessarily continuous tree cover was most utilised.

Taking both habitat type and broad-leaved tree cover into account also showed composition of individual MCP areas was significantly different from the colony MCP whereas composition within core areas was not significantly different from individual MCPs (weighted mean Wilks' $\Lambda = 0.0402$, $\chi^2 = 115.6659$, d.f. = 22, $p < 0.0001$, randomisation $p = 0.001$; weighted mean Wilks' $\Lambda = 0.0418$, $\chi^2 = 114.2988$, d.f. = 22, $p < 0.0001$, randomisation $p = 0.146$). The simplified rank is provided in Table 5.2c. Again broad-leaved woodland was the most utilised habitat type. In general pasture fields with a high level of tree cover were higher up in the simplified rank, with arable fields least utilised.

Mean field size (±SD) for each field type and landscape is provided in Figure 5.4. The general linear model indicated field size (log transformed) varied between landscapes (GLM, $F_{2,1317} = 92.96$, $p < 0.001$) and was affected by field status (GLM, $F_{3,1317} = 32.63$, $p < 0.001$). Multiple comparisons indicated that field sizes in the high quality locality were significantly smaller than those in the lowland and upland. Arable fields were significantly larger than pasture fields, with pasture fields significantly smaller than pasture+ fields overall.

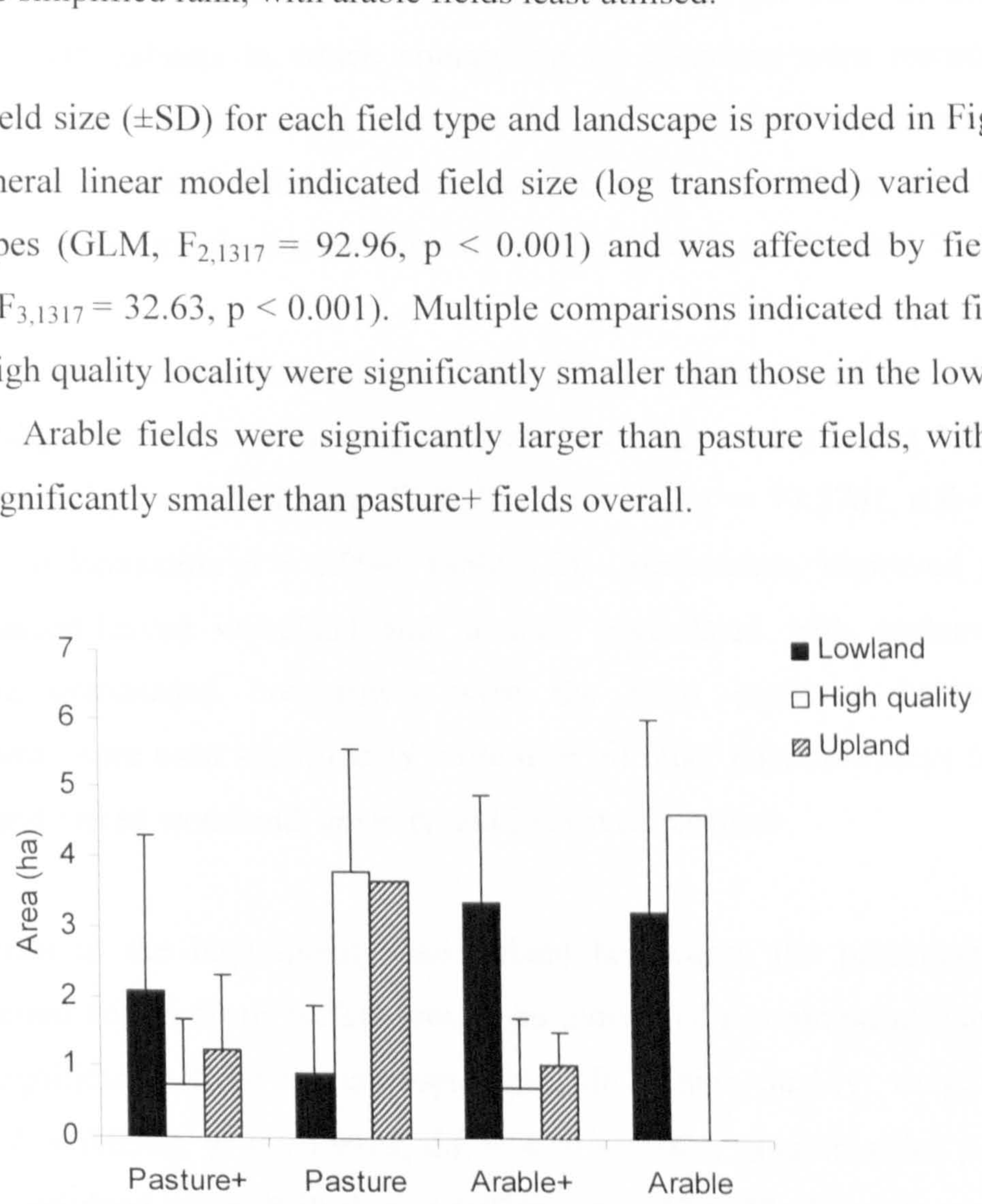

Figure 5.4. Mean (±SD) field size for pasture (improved and semi-natural grassland) and arable fields in the 2 km radius around the *Rhinolophus hipposideros* maternity roosts in lowland, high quality and upland landscapes. +, fields with tall, unmanaged hedgerows or woodland on one or more of their boundaries compared with those with only managed or largely defunct hedges, fences or stone walls.

Commuting behaviour

A total of 301 commuting fixes were recorded across the three localities during the tracking study. In the lowland landscape the locations of commuting fixes were mainly in pasture with unmanaged hedges (32 %), settlements (26 %), broad-leaved woodland (15 %) and improved pasture with managed hedges (10 %). In the high quality landscape the predominant habitats in which commuting fixes were recorded were pasture with unmanaged hedges (36 %), broad-leaved woodland (35 %) and settlements (including gardens) (24 %). In the upland landscape the habitats in which commuting fix locations were recorded were mainly pasture with unmanaged hedges (54 %), coniferous woodland (17 %), semi-natural grassland with unmanaged hedges (9 %) and settlements (8 %). The remaining 12 % comprised broad-leaved woodland, water and bracken/heath.

The percentage habitat composition within 50 m buffers around an individual's commuting fixes was significantly different from the corresponding MCP at the lowland locality (weighted mean Wilks' $\Lambda = 0.0506$, $\chi^2 = 77.5761$, d.f. = 13, $p < 0.0001$, randomisation $p = 0.004$; Table 5.2). Settlements, improved pasture+, water, broad-leaved woodland and amenity (associated with settlements and featuring unmanaged hedgerows) were the most preferred habitat types. Settlements were used significantly more than all other habitats except for broad-leaved and mixed woodland, amenity and improved pasture+.

In contrast in the high quality and upland landscapes the percentage habitat composition within 50 m buffers around an individual's commuting fixes did not differ significantly from the corresponding MCP (high quality: weighted mean Wilks' $\Lambda = 0.0302$, $\chi^2 = 20.9919$, d.f. = 4, $p < 0.001$, randomisation $p = 0.139$; upland: weighted mean Wilks' $\Lambda = 0.0266$, $\chi^2 = 32.6377$, d.f. = 6, $p < 0.0001$, randomisation $p = 0.221$).

5.4.2 *Landscape use*

The utilisation distribution (point pattern of fix locations) of all bats tracked per locality displays evidence of strong spatial contagion in each landscape. At different spatial scales a similar pattern occurs implying the pattern is scale invariant (refer to Figure 5.5 for example). The linear log-log plots derived from the box-counting confirm the point patterns are fractal and gives the following value for the fractal dimension, lowland D = 1.324, high quality D = 1.192, upland D = 1.218. This implies that the point pattern of fix locations for the colony is most clumped in the high quality locality and most dispersed in the lowland locality.

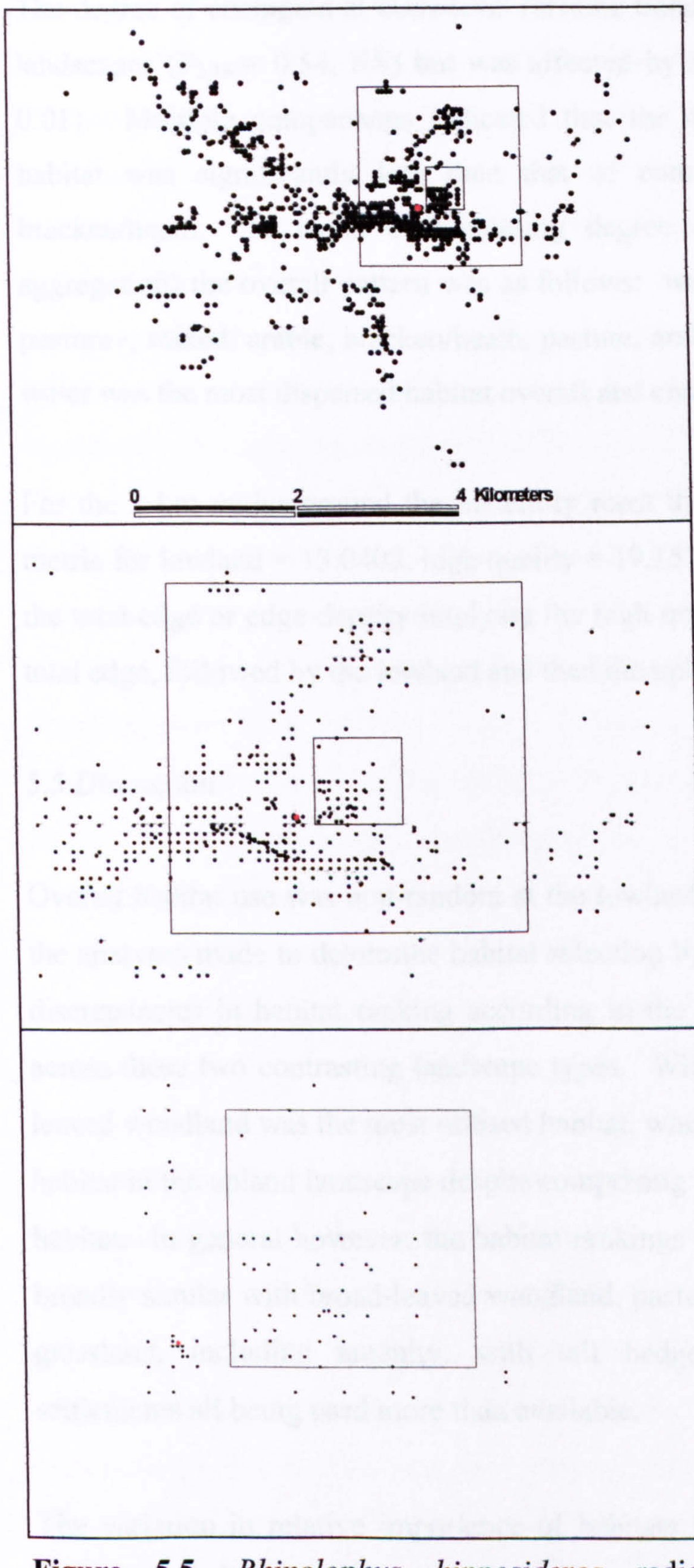

Figure 5.5. *Rhinolophus hipposideros* radio-tracking fixes within the lowland locality at three spatial scales, with successive magnification (top to bottom). A similar pattern occurs illustrating a scale invariant or self-similar, point pattern. Maternity roost (●) is shown.

The degree of contagion at class-level (arcsine transformed) did not vary between landscapes ($F_{2,16} = 0.54$, NS) but was affected by habitat type ($F_{9,16} = 4.16$, $p < 0.01$). Multiple comparisons indicated that the degree of contagion of water habitat was significantly less than that of coniferous, arable+, pasture and bracken/heath. In terms of increasing degree of contagion (i.e. increasing aggregation) the overall pattern was as follows: water, settlements, broad-leaved, pasture+, mixed, arable, bracken/heath, pasture, arable+, coniferous, implying that water was the most dispersed habitat overall and coniferous the most clumped.

For the 2 km radius around the maternity roost the landscape shape index (LSI) metric for lowland = 13.0402, high quality = 19.1570, upland = 8.4754. LSI gives the total edge or edge density implying the high quality landscape has the greatest total edge, followed by the lowland and then the upland localities.

5.5 *Discussion*

Overall habitat use was non-random at the lowland and upland localities although the analyses made to determine habitat selection by *R. hipposideros* showed some discrepancies in habitat ranking according to the relative importance of habitats across these two contrasting landscape types. Within the lowland locality broad-leaved woodland was the most utilised habitat, whereas water was the most utilised habitat in the upland landscape despite comprising less than 1 % of the surrounding habitat. In general however, the habitat rankings across these two landscapes are broadly similar with broad-leaved woodland, pasture+ (improved and semi-natural grassland, including amenity, with tall hedgerows/adjacent woodland) and settlements all being used more than available.

The variation in relative importance of habitats is reflected in the results of the dietary analysis undertaken concurrently with the radio-tracking study (Chapter 2). Here I found that variations in habitat and landscape around roosts have an influence on faecal composition. The importance of riparian habitat in the upland landscape for example is echoed by the abundance of Trichoptera in the diet in this locality which is characterised by numerous small streams that drain through the valleys from the higher moorland and generally feature continuous bankside tree

cover. All but one species of this family in Britain have aquatic larvae and newly emerged adults can be seen in large numbers over the water, often in small swarms (Chinery 1993). Some of the Trichoptera larvae live preferentially or exclusively on submerged tree roots (Kirby 2001) which may help explain the importance of this habitat in this locality. In addition water quality would be expected to be higher in the upland landscape as the numerous small streams drain down from the higher moorland. Water quality is also known to affect activity of some bat species, for example *Pipistrellus* sp. (Vaughan et al. 1996) so its effect on *R. hipposideros* warrants further investigation.

The importance of broad-leaved woodland as a foraging habitat for *R. hipposideros* has previously been recognised in both early acoustic surveys (Gaisler 1963b, Schofield 1996) and more recent radio-tracking studies (Bontadina et al. 2002, Schofield et al. 2002) with the species traditionally being described as a woodland specialist. Furthermore, studies by Schofield (1996) in Britain and Reiter (2004a) in Austria concluded that woodland is an important factor explaining the distribution and selection of maternity roosts for the species. However my study has demonstrated that geographical variation in habitat selection does exist and that broad-leaved woodland may not necessarily be the key habitat type surrounding all roosts.

The preference for settlements is more surprising. Built up areas are avoided by other rhinolophids. Urban areas were found to be the least important habitat for *R. ferrumequinum* (Duvergé and Jones 2003) and *R. euryale* (Russo et al. 2002). Urban areas are also negatively selected by *Myotis myotis* (Drescher 2004) and *Myotis yumanensis* (Evelyn et al. 2004). However many other vespertilionid species exploit suburban and urban areas, for example *Pipistrellus pygmaeus* (Davidson-Watts et al. 2006), *Nyctalus noctula, Vespertilio murinus, Eptesicus nilssonii* (Rydell 1992).

In Chapter 4 I showed that at least two-thirds of alternative day and night roosts used by *R. hipposideros* during the radio-tracking study occurred within the settlement habitat type and that night roosts were significantly nearer to core home range areas, with 56–64% of night roosts actually contained within core nuclei.

Settlements are therefore of importance in rural areas in terms of providing both foraging and roosting opportunities. However the result must be interpreted with care. Although flying species of vertebrates may be less affected by urbanisation since they can move more readily between patches than non-volant species (Gilbert 1989), in general urbanisation is detrimental to insectivorous bat communities (Kurta and Teramino 1992, Gaisler et al. 1998, Avila-Flores and Fenton 2005). The built-up areas within the three study landscapes are characterised by their longevity, small extent and disaggregated nature, as revealed by the class-level analysis, and are analogous with historic dispersed or nucleated settlements (Aston 1985). For example many properties within the high quality landscape originated as early 19th century small-holdings and those in the lowland study area have their antecedents as medieval dispersed hamlets and farmsteads (Aston 1987). Larger towns and cities would be avoided by the species.

The preference for settlements may relate in part to the level of tree cover. The majority of the close approach radio-tracking fixes (±10 m) were associated with tree cover (refer to Chapter 3), including those in the settlement habitat type. The analyses made to determine habitat selection in terms of tree cover at the lowland locality showed that 76–90 % tree cover was the most utilised in both levels of analysis. Zero tree cover was the lowest ranked in the selection of home ranges whilst continuous tree cover (91–100 %) was the lowest ranked in the selection of core areas. Overall, tree cover of 26–90 % was used more than available in the core areas. This pattern is also demonstrated when combining level of tree cover with habitat type. Although broad-leaved and mixed woodland types were the most utilised, pasture fields with over 25 % associated tree cover and settlements with 1-10 % and 26-75 % associated tree cover were also selected for above their availability.

This implies that tree cover, and not necessarily woodland *per se*, and edge habitats are of key importance for *R. hipposideros*. A preference for habitats with a high edge effect has been found in other rhinolophids, for example *R. ferrumequinum* (Duvergé 1996), *R. mehelyi* (Russo et al. 2005) as well as a range of other insectivorous bat species, for example *Pipistrellus* spp. (Downs and Racey 2006). A recent study by Lumsden and Bennett (2005) in south-eastern Australia found

that scattered trees in farmland are used extensively by bats as foraging habitat. They recorded highest activity at density of 20-30 trees/ha, which corresponds to densely scattered trees, and found activity was comparatively less in woodland blocks. Similarly Grindal and Brigham (1998) found that small forest openings may lead to an increase in bat activity whilst sheltered and sunny open space is of vital importance to many woodland invertebrates (Kirby 2001).

Given the importance of edge features, the landscape shape metric is ecologically relevant to *R. hipposideros* and reflects an important attribute of spatial pattern for the species. The results of the landscape analysis indicated that the greatest total edge occurred in the high quality landscape, followed by lowland then upland. The landscape shape index metric can also be interpreted as a measure of patch aggregation or disaggregation (McGarigal et al. 2002). Specifically, as LSI increases, the patches become increasingly disaggregated. In the high quality landscape broad-leaved woodland, pasture fields with adjacent tall hedgerows/ woodland and settlements comprised 81 % of the 2 km radius around the roost compared with 51 % and 33 % in the lowland and upland localities respectively. In addition field size was significantly smaller in the high quality landscape. Pasture+ fields comprised 42 % of the area surrounding the roost, with an average field size of 0.75 ha, so overall tree cover was much greater. Therefore the high quality landscape was characterised by an abundance of preferred habitats, which were well dispersed across the area surrounding the roost. This could explain why, in contrast to the lowland and upland localities, there was no significant difference between the percentage habitat composition of used and available areas within the high quality landscape.

In Chapter 3, I estimated the foraging density of bats within 2 km of the maternity roost to be 0.09 bats/ha for the upland locality, 0.13 bats/ha for the lowland and 0.50 bats/ha for the high quality landscape. The estimated foraging density of *R. hipposideros* in the three landscapes and overall colony sizes are reflected in both increasing coverage of preferred habitats and increasing edge.

The observed patterns of the utilisation distribution display evidence of spatial contagion in each landscape, or self-similarity. Such self-similarity is required to

extrapolate mechanisms from a small to a large spatial scale (Sugihara and May 1990) and should be tested prior to the calculation of the fractal dimension (Turchin 1996). The utilisation distribution is most dispersed in the lowland landscape and most clumped in the high quality locality. Haskell *et al.* (2002) state that mounting evidence suggests that resource distributions also typically exhibit statistically similar patterns over 2-3 orders of magnitude. Assuming utilisation patterns reflect resource distribution the resource density is highest in the high quality landscape and lowest in the lowland landscape.

Reiter (2004a) showed that in Austria large colonies of *R. hipposideros* relied on large woodland areas, whereas a low coverage of woodland supported small colonies. This is supported by the maternity roosts used in the present study, with increasing coverage of broad-leaved woodland reflected in greater colony sizes. However it is noteworthy that in the high quality landscape much of the extensive tracts of woodland features continuous tree cover. The landscape shape index metric indicated that the greatest total edge occurred in the high quality landscape, with increasing edge reflecting higher colony sizes. Therefore I suggest that other environmental variables such as level of tree cover and/or availability of edge habitats may be more closely correlated with the carrying capacity of a given area and this warrants further investigation.

The large sample sizes involved in this study have allowed an assessment of seasonal changes in habitat selection to be made within the lowland locality. On a broad scale the percentage habitat composition of used and available areas was significantly different for adult female bats pre-parturition and post-parturition. At the finer scale, only adult females post-parturition were found to select habitats within core areas, whereas females during pregnancy used habitats in their core areas according to availability. Broad-leaved woodland and pasture+ fields were most preferred post-parturition.

These discrepancies may relate to changes in energy requirements throughout the breeding season, with habitat selection in core areas corresponding with times of highest energy requirements. Energy demands in female bats continue to rise during pregnancy and lactation reaching a peak during late lactation (Speakman

and Racey 1987, Kurta et al. 1989, McLean and Speakman 2000). This higher energy requirement was reflected in changes to the proportion of night time spent flying, with lactating *R. hipposideros* flying significantly proportionally longer than adult females in early pregnancy and post-lactation (Chapter 3).

The bats may be responding to the availability of prey at certain times of year. However although there was highly significant variation between pre- and post-parturition diet at each locality there was little consistency within individual prey categories and no prey category was constantly observed significantly more than expected in either the pre- or post-parturition diet (Chapter 2). Scatophagidae, one of the major prey categories recorded in the diet, was closest to showing a consistent trend. It was always observed less than expected in the pre-parturition diet and more than expected post-parturition, although differences were not significant for the lowland and upland localities in 2005. Scatophagidae, together with Sphaeroceridae which was also present in the diet, are frequently associated with dung (Chinery 1993). Although broad-leaved woodland was the most utilised habitat post-parturition and used significantly more than pasture+, pasture+ was used more than available which may explain the trend for increased presence of Scatophagidae in the diet at this time. In general therefore it seems likely that bats may have used a greater number and/or diversity of foraging sites early in the breeding season to counteract the lower abundance of insects at that time of year.

The results imply that nulliparous females utilised habitats according to availability and this may be a result of reduced energy demands given that energy requirements in non-reproductive females are considerably lower than in reproductive animals (McLean and Speakman 1999). However the sample of nulliparous females was too small to separate into different time periods so data were pooled across the breeding season, which may have masked habitat selection. In addition, whilst Aebischer *et al.* (1993) state that a minimum of 6 radio-tagged animals should be used for comparison of utilised with available habitats they recommend that for comparisons between categories of animals, each category should exceed 10 individuals. Therefore more work is required to sample increased numbers of bats throughout the breeding season to test these results further.

Juveniles were also found to use habitats according to availability. In 5 of the 6 juveniles radio-tracked I observed a general trend of increasing home range size with time, with home ranges for 3 individuals not reaching asymptotes by the end of the tracking session (Chapter 3). Early flights were characterised by their short duration and limited range, with foraging fixes restricted to broad-leaved woodland or settlements (the immediate area around the roost). The subsequent expansion of ranges corresponded to utilisation of a wider range of habitats. This expansion in range may have obscured any habitat selection during early flights and I therefore postulate that prior to weaning, habitat use in juvenile *R. hipposideros* is probably not random, with broad-leaved woodland being selected. A similar pattern has been recorded in juvenile *R. ferrumequinum* (Duvergé and Jones 1994, Jones et al. 1995). Upon first leaving the maternity roost they spent most of their time foraging on pastures close to the roost, until they were 45-50 days old, corresponding to time of weaning, and by the time they were 60 days old they had expanded their foraging range and exploited different types of feeding areas.

Implications for conservation

European farming practices have become increasingly intensive in the post-war period, with a dramatic reduction in landscape diversity (Robinson and Sutherland 2002). This period corresponds with the documented large-scale decline of the study species (Stebbings 1988). In Britain *R. hipposideros* has undergone a contraction in range (Mitchell-Jones 1994-1995) and is now confined to south-west England and Wales (Richardson 2000). Given the general avoidance of arable habitats by the species recorded in this study, and also by Cresswell Associates (2004) it may be that the contraction in range reflects the increasing homogeneity of the landscape and polarisation of agriculture in Britain. Arable farming now dominates in the east and pastoral farming in the west (Macdonald and Tattersall 2001). However more recently evidence suggests that the population of *R. hipposideros* is now increasing in Britain (Bat Conservation Trust 2004). This is despite the fact that regionally there was significantly less improved grassland in 1998 than 1990 in the western lowlands of England and Wales, and significantly more arable (Haines-Young et al. 2000). However Robinson and Sutherland (2002) postulate that whilst reduction in habitat diversity was an important driver

for biodiversity loss in the 1950s and 1960s, reduction in habitat quality is now probably more important. Loss of hedgerows and hedgerow trees may also be implicated in the decline. Traditionally, hedgerow trees would have occurred at much greater densities, for example 2.5 trees per acre of farmland were estimated in 1951 but in the mid-1970s an average of just 0.28 per acre was recorded (Rackham 1986).

Organic farming methods approximate more closely with the traditional heterogeneous lowland landscape. Organic farms are characterised by more complex crop rotations, greater proportion of land that is grass rather than arable land, greater density of hedges, and higher and wider hedges (Feber et al. 1997, Feber et al. 1998). However despite the difference in hedge structure and density, Fuller *et al.* (2005) found that there were no significant differences between systems in the numbers of trees recorded in hedges. In a comparison of matched pairs of organic and conventional farms Wickramasinghe *et al.* (2003) only recorded *R. hipposideros* on organic farms. However in my study radio-tracked *R. hipposideros* showed no preference for organic farmland over conventionally farmed land within the lowland landscape. Therefore organic farming *per se* may not necessarily reflect the best management practice for the species. Although insect abundance, richness and moth species diversity is higher on organic farms (Wickramasinghe et al. 2004), for *R. hipposideros* suitable habitats for foraging are required above all.

Andrén (1994) has suggested that the total area of key suitable habitat would be more important than the spatial arrangement of blocks to the species concerned, as long as the key habitat made up more than 30 % of all available habitats. Although this is the case in each of the landscapes studied, connectivity is also of high importance to *R. hipposideros* with movement generally along or within vegetation cover. Effective conservation of bats requires a landscape-based approach (Racey and Entwistle 2003). Therefore management should focus on increasing the extent and quality of the key habitats, broad-leaved woodland and pasture+ fields, and overall tree cover within the 2 km radius around maternity roosts (refer to Chapter 3), whilst maintaining and enhancing the overall connectivity of the landscape. Specific management prescriptions are provided in Appendix 3.

CHAPTER SIX

GENERAL DISCUSSION

6 General discussion

6.1 *Outcome of the study*

The loss or modification of semi-natural habitats and pesticide use associated with agricultural intensification are considered primary factors in the reduction of many European bat populations since the 1940s (Stebbings 1988, Hutson 1993, Walsh and Harris 1996b). *R. hipposideros* has become virtually extinct in large areas of north-west Europe and whilst it has also undergone a contraction in range in Britain, the British and Irish populations are now considered significant in a European context. In Britain, populations are found within both intensively managed and traditionally managed lowland, together with upland. This has enabled me to undertake an extensive study of a vulnerable temperate bat species in which both spatial and temporal differences in behaviour and habitat use have been investigated and in particular to consider the differences in foraging behaviour within an intensively managed and traditionally managed agricultural landscape.

In Chapter two, I showed that whilst the composition of the diet of the species was fairly consistent in terms of major prey categories consumed, the diet did vary significantly between landscapes. These differences are likely to be due to variation in habitat specific to each locality, as they were more pronounced between the lowland and high quality landscapes, and lowland and upland. Interestingly, despite differences in the diet composition, in chapter three I determined that the behaviour of *R. hipposideros* was consistent across the three landscapes with no significant difference between the majority of parameters investigated, including home range and mean maxiumum distance. This result is suprising as bats in larger colonies would be expected to show either increased foraging ranges because of higher levels of intraspecific competition for food resources around the roost, or reduced foraging ranges because roosts in high quality habitat contain higher levels of food that bats would not need to travel so far to obtain. Therefore it seems likely that *R. hipposideros* are adopting an optimal behaviour that is constrained by the species' morphology, regardless of the

surrounding landscape. In accordance with optimum foraging model, poor habitat quality would result in animals using larger foraging areas and/or spending longer to forage (Stephens and Krebs 1986). Whilst total flying time did not vary among landscapes I did find that the first flying bout was significantly longer in the lowland landscape. Furthermore, in contrast to previous studies I found that colder temperatures and increasing rainfall resulted in bats flying for longer than usual. The bats may aim to reach a target of energy consumption, and reaching this target takes longer in poorer conditions. In chapter four I showed that increased rainfall and stronger winds were also associated with shorter night roosting bouts. Insectivorous bats typically display a bimodal pattern of overnight activity whereas *R. hipposideros* exhibited multimodal patterns. *R. hipposideros* may deviate from the more typical pattern as their broad diet and ability to feed both by gleaning and aerial hawking allows them to feed throughout the night. This may also explain why the species does not follow the more typical pattern of reduced activity in colder temperatures. Numbers of flying insects have been shown to be significantly reduced on nights when dusk temperature falls below 10°C (Rydell 1989) and yet *R. hipposideros* would still be able to forage successfully on insects and non-volant prey resting on vegetation and on moths. However when considering the diet and overnight activity patterns, I believe gleaning is unlikely to be the principal foraging strategy with the majority of prey caught on the wing during aerial hawking. Species that appear to be adapted primarily for manoeuvrable flight in clutter may be able to reduce foraging flight costs, without increasing foraging time and decreasing insect encounter rates, by flying in insect concentrations that form outside cluttered areas, for example insect swarms (Aldridge and Rautenbach 1987). Therefore feeding on swarming insects at dusk and dawn could play an important part in foraging.

Over three-quarters of the bats night roosted away from the maternity roost, typically in buildings. By determining spatial relationships between roosts and foraging areas, I tested the hypothesis that night roosts serve as refuges in close proximity to key foraging sites, and are therefore of considerable conservation value. Night roosts were significantly nearer to core foraging areas than the maternity roost, with over half actually located within core areas. Minimisation of distance to feeding sites may be the primary function of the night roosts, being

used for resting and digestion between foraging bouts and they may form an integral part of the core foraging areas and need to be protected. Many of the night roosts were also used for day roosting, with roost switching most frequently recorded in breeding females during early pregnancy and post-lactation and in nulliparous females. These roosts are therefore also of importance outside the key maternity period by reducing commuting costs to foraging areas at a time of typically reduced food availability and/or poorer foraging conditions.

As bat populations are likely to be resource limited (Findley 1993) then the amount of suitable habitat around maternity roosts could determine colony size. In chapter five I showed that resource density was lowest in the lowland landscape and highest in the high quality landscape. I showed that both the overall colony sizes and foraging density of *R. hipposideros* in the three landscapes were reflected in both increasing coverage of utilised habitats and increasing edge. Within the high quality landscape, the least fragmented habitat, habitat composition within home ranges was not significantly different from the study area, whereas there were significant differences in the lowland and upland. In addition the distribution of roosts around the maternity roost was uniform, whereas a restricted distribution occurred in lowland and upland. Therefore both habitat and the availability of day/night roosts around the maternity roost may be limiting factors on colony sizes. In common with the diet, geographical variation in habitat selection also exists. Broad-leaved woodlands, water, rural settlements and pasture fields with wooded edge or unmanaged hedges were most utilised. The accurate description of habitat requirements for bats is a key part of their conservation management (Walsh and Harris 1996a) and I determined that broad-leaved tree cover and edge habitats and not necessarily woodland *per se*, are likely to be of key importance for *R. hipposideros*.

My study has shown that organic farming may not necessarily the best management practice for *R. hipposideros* and that suitable habitats for foraging may be required above all. In general organic farms are recognised to be structurally more beneficial. For example a study by Fuller *et al.* (2005) found that the density of hedges was higher on organic than non-organic farms and there were also marked differences in hedgerow structure, with height, base width and top

width all greater on organic farms and more gaps in hedgerows surrounding non-organic fields. However there were no significant differences between systems in the numbers of trees recorded in hedges, which given the highlighted importance of tree cover for *R. hipposideros* in my study, may be key.

The total area of organic farmland relative to non-organic is small (currently 4 % of UK farmland is organic) and an extension of organic farming could contribute to the restoration of biodiversity in agricultural landscapes (Fuller et al. 2005). However a review by Hole *et al.* (2005) suggests that it remains unclear whether a 'holistic' approach (i.e. organic) provides greater benefits to biodiversity than carefully targeted management prescriptions applied to relatively small areas of cropped and/or non-cropped habitats within conventional agriculture. Agri-environment schemes have been used successfully to aid the long-term conservation of a range of species of conservation concern e.g. *R. ferrumequinum* (Longley 2003); Cirl bunting *Emberiza cirlus* (Peach et al. 2001); bumblebees (Pywell et al. 2006); butterflies (Pywell et al. 2004). Previous schemes suggest that a whole farm approach works best (English Nature 2002/2003). In this way key habitats such as tall hedgerows and broad-leaved woodlands can be targeted, together with the overall connectivity of the landscape. Agri-environment schemes that improve matrix quality by 'softening' agriculture could play an important role in reducing fragmentation effects in isolated habitat patches (Donald and Evans 2006) and represent the most viable delivery mechanism for landscape-scale ecological restoration (Vickery et al. 2004). For species such as *R. hipposideros* that are vulnerable to habitat fragmentation (Bright 1993, Henle et al. 2004) this could be critical.

A number of management options are suggested within Appendix 3 based on the findings of the study. The list is not intended to be exhaustive and will require liaison with relevant government and non-government organisations prior to future implementation within appropriate agri-environment schemes (Wales: Tir Gofal and Better Woodland for Wales; England: Higher Level Scheme and Woodland Grant Scheme; see review in Chapter 1, Section 1.3) to ensure proposed measures are both effectual and cost-effective. It is recommended that the findings of this study be supplemented with further radio-tracking work at important colonies of *R.*

hipposideros, as has been done with *R. ferrumequinum* (Robinson et al. 2000, Billington 2004). Furthermore, it is important that the effectiveness of management options be monitored and refined in response to further research (Field et al. 2006). Bat numbers should be monitored long term with respect to any new management measures that are implemented (e.g. via agri-environment schemes), and population trends should be compared with those in replicate (and preferably paired) control areas where targeted management has not been implemented.

Given that a mean maximum distance of 2 km was identified within each of the three contrasting landscapes studied it is recommended that habitat management and improvement works be focussed in this zone around maternity roosts for maximum cost effectiveness. This area can be classified as the 'roost sustenance zone' (Ransome 1996). Where funds are limited then efforts should be concentrated in the 1 km radius around the roost, as, on average, bats spent half of their time in this zone. This zone is also likely to be of greater importance to juveniles prior to weaning and can be classified as the 'juvenile sustenance zone' (Ransome 1996). However it is also important that the wider landscape should also be taken into account to aid gene flow among metapopulations. It is also vital that existing night-roosts and alternative day roosts be retained until we have a greater understanding of the impact their loss would have both on the individual(s) concerned and in terms of the cumulative effect on the maternity colony, particularly given the loyalty of *R. hipposideros* to these roosts and the potential for them to form an integral part of the core foraging areas and for kin-related use.

6.2 *Implications for future research*

The techniques involved in radio-tracking studies are necessarily invasive and expensive but can be effective in determining foraging zones and additional roost sites. However they must be used with caution. It is necessary to legitimise the potential disturbance before embarking on such studies. It is also vital that the results of such research, including small-scale studies commissioned for development purposes, are in a format that contributes to and extends the knowledge base for the species, and allows comparison of behaviour among

geographical areas and reproductive statuses. I recommend minimum outputs for each tracked individual are: home range (based on minimum convex polygons), maximum distance travelled from roost and mean length of first foraging bout. More information on habitat use determined by compositional analysis would also be helpful.

The reasons behind use of night and alternative day roosts for this species need to be more fully understood, particularly as they are typically in buildings which can lead to conflict. Feeding habitat may be important for selection of night roosts but conversely, feeding habitat may equally be constrained by availability of night roosts. Availability of suitable night roosts could therefore represent a constraint on the population size of *R. hipposideros*.

It would be pertinent to sample increased numbers of bats throughout the breeding season to test habitat use and selection further. Further work is also recommended to determine whether level of broad-leaved tree cover and/or availability of edge habitats are more closely correlated with the carrying capacity of a given area than the extent of broad-leaved woodland *per se*.

In conclusion, this study has contributed a great deal of information on *R. hipposideros* behaviour. The findings provide the most detailed account of foraging behaviour to date, as well as the most extensive analysis of the summer diet undertaken in Britain. The relevance of the results of this study are not limited to the study areas but have significance for assessing this species within the remainder of Britain and Europe. As with much work of this nature, it has also presented several aspects that need further research. An important feature of the study has been to place the findings in the context of their implications for its conservation. The successful use of agri-environment schemes in order to improve habitat around known maternity colonies of the endangered *R. ferrumequinum* in south-west England has demonstrated that such studies can be fundamental to the long term improvement in the conservation status of species.

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APPENDICES

1 Biometric data recorded from captured *R. hipposideros* during the three-year radio-tracking study.

2 Day and night *R. hipposideros* roosts identified during the three-year radio-tracking study.

3 Management prescriptions.

Appendix 1

ID	Date	Age	Sex	Repcon	FA/mm	Weight/g	Tag	Notes
								Lowland A 2003
	20/05/03	2	2	1	37.40	5.00		
Y1001	20/05/03	3	2	2	36.40	5.45	173.207	Poorly
Y1002	20/05/03	3	2	2	37.60	5.40	173.265	Minxy (recaught by GJ on 19/05/05 FA38.00; 5.4g; no wing/tag damage)
	29/05/03	3	2	3	36.00	6.10		
	29/05/03		1	8	37.10	4.10		
Y1003	29/05/03	3	2	3	38.60	5.10	173.247	Woody
Y1004	29/05/03	3	2	3	37.60	6.35	173.227	Backtrack
	29/05/03		1	8	36.00	4.35		
	29/05/03		1	8	36.90	4.60		
Y1005	08/06/03	3	2	3	38.70	6.50	173.239	Houdini
Y1006	08/06/03	3	2	3	38.60	6.40	173.255	Dewy (recaught by GJ on 19/05/05 FA38.50; 5.2g; no wing/tag damage)
Y1007	08/06/03	3	2	3	38.60	6.80	173.733	Rooster (recaught 03/05/04; no wing/tag damage; recaught 16/08/04 lacated)
	08/06/03	3	2	3	37.80	6.80		
	08/06/03	3	2	3	38.50	6.70		
	22/07/03	2	2	4	37.20	5.40		
Y1008	22/07/03	2	2	4	38.90	5.10	173.288	Laurel (found injured by roost 29/08/04, died; false teats now present+lactated)
Y1009	22/07/03	3	2	5	37.30	5.80	173.335	Queeny
	22/07/03	3	2	5	37.30	5.40		
	22/07/03	3	2	5	38.50	4.80		
	22/07/03	3	2	5	37.10	5.30		
Y1010	22/07/03	3	2	5	37.40	5.50	173.721	Speedy (recaught 03/05/04; no wing/tag damage)
	22/07/03	3	2	5	39.30	5.65		
	12/08/03		1	8	35.60	5.10		
Y1011	12/08/03	3	2	4	37.70	5.80	173.323	Creeping Jenny (recaught by GJ on 19/05/05 FA37.8; 5.8g; no wing/tag damage)
	12/08/03		1	8	36.10	5.00		
	12/08/03	3	2	5	36.55	5.50		

ID	Date	Age	Sex	Repcon	FA/mm	Weight/g	Tag	Notes
								Lowland A 2003
	12/08/03		1	8	36.45	4.90		
Y1012	12/08/03	1	1	8	36.60	5.00	173.49	Jude (recaught 03/09/03; tag still attached - released immediately)
	12/08/03	3	1	8	36.30	4.80		
Y1013	12/08/03	2	2	4	37.15	5.35	173.709	Jane Grange
Y1014	02/09/03	1	2	7	38.20	4.90	173.276	June
	02/09/03		1	8	36.60	4.50		
	02/09/03		1	8	37.10	4.80		
	02/09/03		1	8	37.20	4.50		
	02/09/03		1	8	38.10	5.10		
	02/09/03	1	2	7	36.15	4.50		
Y1015	02/09/03	2	2	4	37.60	4.90	173.346	Buzby (recaught by GJ on 19/05/05 FA37.6; 4.9g;no wing/tag damage)
Y1016	02/09/03	2	2	7	38.50	5.40	173.698	Chestnut (recaught 12/03; recaught 03/05/04; no wing/tag damage)

ID	Date	Age	Sex	Repcon	FA/mm	Weight/g	Tag freq	Notes
								Lowland A 2004
Y1017	03/05/04	3	2	3	38.10	4.25	173.193	Sandy (V small false teats)
	03/05/04	2	2	2	37.10	4.75		
	03/05/04		1	8	37.10	3.50		
Y1018	03/05/04	3	2	3	37.10	4.75	173.311	Danni
	03/05/04	2	2	2	37.60	4.50		
	03/05/04	2	2	2	38.40	4.00		
	03/05/04	2	2	2	37.70	4.00		
Y1019	10/05/04	3	2	3	38.60	6.00	173.248	Rowan (recaught 02/08/04; fur regrown, now lactating; no RD)
Y1020	10/05/04	3	2	3	37.20	6.00	173.302	Dolly
Y1021	10/05/04	3	2	3	37.00	4.75	173.733	Ashley
	10/05/04		1	8	37.00	4.50		
	10/05/04	3	2	3	38.00	4.50		
	10/05/04	2	2	2	37.80	3.50		
	10/05/04	2	2	2	37.30	3.50		
	10/05/04	3	2	2	37.50	3.60		
Y1022	21/05/04	3	2	3	37.80	5.50	173.288	Little Miss Predictable
Y1023	21/05/04	2	2	2	37.50	4.00	173.744	Dusty
	21/05/04	3	2	3	36.30	5.75		
Y1024	21/05/04	3	2	3	37.80	6.25	173.335	Brook (recaught by GJ on 19/05/05 FA38.55; 5.5g; some blister on wing)
	02/08/04		1	8	36.50	4.10		
Y1034	02/08/04	3	2	5	35.70	4.70	173.318	Maisey
	02/08/04	2	2	4	37.20	4.50		
	02/08/04	3	2	4	38.55	4.30		
	02/08/04		1	8	36.30	3.90		
Y1032	02/08/04	3	2	5	38.10	5.00	173.207	Milly
	02/08/04	2	2	4	38.30	3.50		
Y1033	02/08/04	3	2	5	38.20	4.30	173.231	Riff Raff
	02/08/04		1	8	35.70	3.90		
	02/08/04		1	8	36.00	3.80		

ID	Date	Age	Sex	Repcon	FA/mm	Weight/g	Tag freq	Notes
								Lowland A 2004
Y1007	16/08/04	3	2	6	38.60	5.90		Fur regrown, no RD
	16/08/04		1	8	35.90	4.90		116 counted out, 12+ in MR
Y1035	16/08/04	1	1	8	36.70	4.50	173.201	Mr Squelchy
Y1036	16/08/04	3	2	6	37.40	5.90	173.246	Grace (subsequently found dead in roost; antenna caught in ridge beam)
	16/08/04	1	1	8	36.30	4.40		
	16/08/04		1	8	35.50	3.90		
Y1037	16/08/04	3	2	6	37.50	4.50	173.272	Lyn (fur still bare around nipples)
	16/08/04	2	2	6	36.80	4.70		
	16/08/04	1	1	8	36.05	4.40		
Y1038	16/08/04	2	2	7	38.50	5.20	173.303	Apple (recaught by GJ on 19/05/05 FA38.6; 5.8g; discoloured around wing)
	16/08/04		1	8	36.40	4.50		
	16/08/04		1	8	n/a	n/a		Released on capture
	16/08/04		1	8	n/a	n/a		Released on capture
	16/08/04		1	8	n/a	n/a		Released on capture
	16/08/04		1	8	n/a	n/a		Released on capture

ID	Date	Age	Sex	Repcon	FA/mm	Weight/g	Tag freq	Notes
								Lowland A 2005
Y1048	29/7/05	3	2	5	36.60	5.40	173.266	Skinny (143 counted between 21:16-21:45)
	29/7/05	3	2	5	37.10	5.10		
	29/7/05	3	2	4	36.90	5.50		
	29/7/05		1	8	n/a	n/a		released immediately
	29/7/05		1	8	n/a	n/a		released immediately
Y1152	07/08/05	3	2	5	38.10	5.90	173.302	Star
	07/08/05	3	2	5	38.10	5.80		
	07/08/05	3	2	5	37.10	5.40		
Y1154	07/08/05	3	2	5	38.10	6.00	173.744	Gracie (big false nipples)
Y1153	07/08/05	3	2	5	36.50	6.00	173.334	Bunny (nipples not as bare as others)
	07/08/05	1	1	8	35.60	4.90		
Y1049	07/08/05	1	1	8	36.30	4.90	173.207	Dippy
Y1050	07/08/05	1	2	4	36.70	5.20	173.255	Girl
Y1151	07/08/05	1	1	8	36.40	4.60	173.287	Boy

ID	Date	Age	Sex	Repcon	FA/mm	Weight/g	Tag freq	Notes
								High quality B 2004
Y1025	07/06/04	3	2	3	37.90	4.50	173.212	
Y1026	07/06/04	3	2	3	37.80	5.40	173.235	Sylvia
	07/06/04		1	1	36.30	3.50		
	07/06/04		1	1	36.90	3.50		
Y1027	07/06/04	3	2	3	39.4	6.00	173.306	Cedar
	12/06/04	3	2	3	38.80	6.75		
	12/06/04		1	1	36.50	4.40		
	12/06/04	3	2	3	38.40	6.00		
Y1028	12/06/04	3	2	3	37.85	6.00	173.320	Betony (recaught by DP on 27/03/05, no tag/ring damage)
Y1029	21/07/04	3	2	4	38.30	5.40	173.197	Stephie
	21/07/04		1	1	37.10	5.20		
	21/07/04		1	1	35.50	5.10		
Y1030	21/07/04	3	2	5	37.70	6.50	173.294	Merry
Y1031	21/07/04	3	2	5	37.70	6.40	173.341	Poppy
	21/07/04	2	2	4	n/a	n/a		Released on capture
	21/07/04		1	1	37.00	5.00		
Y1039	06/09/04	3	2	6	38.20	5.40	173.197	Honey
	06/09/04	2	2	6	36.60	4.80		
Y1040	06/09/04	3	2	6	37.00	5.10	173.225	Dee
Y1041	06/09/04	3	2	6	37.25	5.70	173.275	Cassie
	06/09/04	3	2	6	36.90	5.90		
	06/09/04	2	2	6	39.60	5.50		Forearm checked twice
	06/09/04		1	1	n/a	n/a		Released on capture
	06/09/04		1	1	n/a	n/a		Released on capture

ID	Date	Age	Sex	Repcon	FA/mm	Weight/g	Tag freq	Notes Upland C 2005
	31/05/05	3	2	3	36.70	6.40		
Y1042	31/05/05	3	2	3	38.40	6.30	173.196	Neu Neu (large false nipples)
Y1043	31/05/05	3	2	3	36.80	5.60		Bonny
	31/05/05	3	2	3	?	5.50		
	31/05/05	2	2	1	36.70	4.80		
	31/05/05	3	2	3	38.50	5.90		
	31/05/05		1	8	36.70	4.75		
	31/05/05	3	2	3	38.10	5.10		
Y1044	31/05/05	3	2	3	38.80	5.20	173.275	Sparky
	31/05/05		1	8	36.60	4.90		
	18/07/05	2	2	4	38.40	5.80		
	18/07/05		1	8	37.20	5.50		
	18/07/05	2	2	4	36.50	5.75		
Y1045	19/07/05	3	2	5	38.20	7.10	173.206	Hermione (recaught on 21/08/05 - no bald patch, darker under fur regrown, no RD)
Y1046	19/07/05	3	2	5	38.90	7.20	173.245	Sunny
Y1047	19/07/05	3	2	5	38.80	7.30	173.305	Nancy Fidget
Y1155	21/08/05	3	2	6	36.90	6.30	173.31	Tilly
Y1156	21/08/05	3	2	6	38.60	6.10	173.216	Cwm-By
Y1157	21/08/05	3	2	6	38.10	6.50	173.413	Beany

KEY: Age: 1 = juvenile; 2 = nulliparous; 3 = adult
Sex: 1 = male; 2 = female
Repcon: 1 = not pregnant; 2 = pregnant (early); 3 = pregnant (late); 4 = not lactating; 5 = lactating; 6 = post-lactating; 7 = post-not-lactating; 8 = male;
FA = forearm;
RD = ring damage;
GJ = Gareth Jones, University of Bristol;
DP = Dave Priddis, Gloucestershire Bat Group

Appendix 2

New roost sites at lowland A locality

Roost type/name	Location	NGR (ST)	Used by	DR or NR?	Notes
Garage, Mendip	Churchill	4553 6040	Y1002	NR	No bats seen during daytime survey
Boiler Room, Langford Court	Upper Langford	4699 6012	Y1002	DR	On 21/5/03 10+ bats present
Wood Shed, Grange Farm	Upper Langford	4597 5957	Y1002 Y1007 Y1013 Y1022 Y1049	NR DR DR & NR NR NR	
Stone Wall Shelter, Old Quarry	Dolebury Wood	4617 5916	Y1003 Y1049	DR DR	Only Y1003 present at 15:00 on 30/5/03
Outbuilding, Rose Cottage	Says Lane	4556 5989	Y1003 Y1008 Y1018 Y1022 Y1036 Y1154	NR DR DR & NR NR DR & NR NR	Owners indicate breeding occurred in past
??, Enderleigh Gardens	Churchill	448 595	Y1006	NR	Exact location not pinpointed
Outbuilding, Ivy Lodge	Front Street, Churchill	4399 5996	Y1006 Y1032	NR NR	Owners have seen LHS previously

Roost type/name	Location	NGR (ST)	Used by	DR or NR?	Notes
Garage, near Doleberrow Rising?	Doleberrow	446 599	Y1006 Y1010	NR DR & NR	1 GHS also recorded
Garage, La Cabana	Lower Langford	4608 6061	Y1007 Y1014 Y1016	NR NR NR	
Outbuilding, Laurel House	Upper Langford	4547 5962	Y1008 Y1009	DR & NR NR	
Small-leaved Lime tree	Dolebury Wood	454 594	Y1008	DR	
Ash tree	Dolebury Wood	4539 5949	Y1008	NR	
Barn, Lower Court Farm	Churchill Green	4326 6029	Y1010	NR	
Stone Barn, Newleaze House/Daniell's Farm	Churchill Green	4326 6006	Y1010	NR	
Garage?, Guild House	Churchill	4346 5954	Y1010	NR	
Oak tree	Churchill Green	4364 6045	Y1010	NR	
Barn, Dinghurst Farm	Churchill	4420 5966	Y1011	DR	

Roost type/name	Location	NGR (ST)	Used by	DR or NR?	Notes
Outbuilding?, Churchill Court	Churchill	436 602	Y1011	NR	Exact location not pinpointed
Water Works	Star	443 586	Y1012	NR	Exact location not pinpointed
Boiler Room, Old Rectory	Rowberrow	4496 5844	Y1015 Y1152	DR & NR NR	Owners indicate breeding occurred in past
??, Lippiat Lane	Shipham	4536 5744	Y1015	NR	Exact location not pinpointed
Garage, The Croftings	Sidcot	4316 5786	Y1017	NR	
Mine, Sandford Hill	Sandford	429 593	Y1017	DR	Exact location not pinpointed
??, Uplands Cottages	Sandford Batch	425 586	Y1017	NR	Exact location not pinpointed
Outbuilding, Chestnut Tree Farm	Churchill	4426 5976	Y1019	NR	
Outbuilding, Knowle Wood Cottage	Knowle Wood	4404 5937	Y1019	DR	
Garage, Dolebury House	Churchill	4502 5943	Y1020 Y1021 Y1036 Y1154	DR & NR DR & NR DR DR	
Barn, Springhead Farm	Upper Langford	4657 5935	Y1023 Y1153	DR & NR DR & NR	At 20:00 on 12 July 2004 45+ bats observed in roost; breeding confirmed

Roost type/name	Location	NGR (ST)	Used by	DR or NR?	Notes
Porch, The Old Courthouse	Upper Langford	4583 5952	Y1032 Y1033	NR NR	
Garage, Waldon Acres	Sandford	4308 5951	Y1037	DR & NR	
Outbuilding, Little Garth	Churchill	4387 5966	Y1038	DR & NR	
Garage, Pitchbury	Churchill Green	4386 6034	Y1038	NR	
Barn?, Churchill Green Farm	Churchill Green	4295 6018	Y1048	NR	
Derelict cottage, Blagdon Water Gardens	Upper Langford	4648 5949	Y1049	NR	
Outbuilding, Fourways	Burrington	4759 5955	Y1153	DR & NR	

New roost sites at high quality B locality

Roost type/name	Location	NGR (ST)	Used by	DR or NR?	Notes
Outbuilding, Hilgay	Brockweir	542 023	Y1026	DR & NR	
Stables, Woodspring	Brockweir	5430 0272	Y1027	DR	
Outbuilding, Hadley	Brockweir	5431 0297	Y1027	NR	
Garage, Briar Bank	Botany Bay	5237 0206	Y1028	NR	At 1930 on 17/6/04 7+ (10?) LHS DR
Stables, Greystoke's House	Sandy Lane, Brockweir	5496 0265	Y1029	NR	
Stephan's Barn, Belmont	Sandy Lane, Brockweir	5473 0236	Y1029	NR	At 2315 on 25/7/04 second bat also present
Cellars?, Woodspring	Brockweir	5427 0270	Y1029	NR	
Derelict Old Mill, CPL Yard	Off Mill Hill, Brockweir	5404 0111	Y1039 Y1040	DR & NR NR	Unsafe to access; bats seen by CPL staff previously; HQ recommended building not be developed due to bats
Railway Tunnel	Tintern	5356 0022	Y1040	NR	At 1700 on 11/5/04 5 LHS DR in tunnel
Lime Kiln, Ash Grove	Miss Graces Lane	5517 9947	Y1040	NR	AT 0432 on 14/9/04 5 LHS NR in left side
Outbuilding?, Maggett Cottages	Off B4228	558 000	Y1040	NR	
Cave?, Shorn Cliff	Plumweir Wood	541 994	Y1040	NR & DR	

Roost type/name	Location	NGR (ST)	Used by	DR or NR?	Notes
Cave?, Shorn Cliff	Plumweir Wood	539 989	Y1041	NR	Approximate location
Chimney of derelict cottage	Spring Farm	5406 0289	Y1041	DR & NR	Not possible to view into chimney due to dense bramble
Cellars, Lymington House	Brockweir	5376 0250	Y1041	DR & NR	At 1500 on 20/9/04 6 LHS DR (inc Y1041)

New roost sites at upland C locality

Roost type/name	Location	NGR (ST)	Used by	DR or NR?	Notes
Barn, Cwm Farm	Llanbedr	2357 2387	Y1042 Y1156	NR DR & NR	
??, up from Ty Croes Farm	Llanbedr	2255 2325	Y1042	NR	Exact location not pinpointed
Outbuilding, Ty Croes Farm	Llanbedr	2330 2286	Y1042	NR	
Barn, Bont	Llanbedr	2402 2258	Y1043 Y1047	DR NR	
Cellar, Blaenau Isaf	Llanbedr	2424 2331	Y1043	DR	
Kennels, Ty Commins	Llanbedr	2322 2427	Y1044 Y1045	DR & NR NR	
Outbuilding, Darren	Llanbedr	2263 2505	Y1044 Y1045 Y1155	NR NR DR & NR	
Stables, Cwm Farm	Llanbedr	2356 2393	Y1045	NR	
Barn, N of Bont	Llanbedr	2404 2273	Y1047	DR & NR	
??, Sunnybank?	Llanbedr	2424 2220	Y1047	NR	Exact location not pinpointed
Barn, Tal-y-maes Farm	Llanbedr	2254 2602	Y1155	NR	

Roost type/name	Location	NGR (ST)	Used by	DR or NR?	Notes
Chimney, derelict Hermitage	Llanbedr	2291 2512	Y1155	DR	
??, opp Ty Commins	Llanbedr	234 242	Y1156	NR	Exact location not pinpointed
Outbuilding, Nantrychain	Llanbedr	2388 2434	Y1157	DR & NR	

Key: DR - Day Roost; NR - Night Roost; LHS – *R. hipposideros*; GHS – *R. ferrumequinum*
NB: Some house owners yet to be contacted

Appendix 3: Management prescriptions

There follows a number of suggested management options based on the findings of the study.

Flight lines

Although bats were observed crossing open spaces, movement was typically along or within vegetation structures such as hedges, tree lines or woodland. Given the vulnerability of *R. hipposideros* to habitat fragmentation it is vital that existing flight lines be preserved.

Connectivity immediately surrounding the roost is particularly essential as bats were only observed crossing open spaces during the night, rather than at dusk and dawn. The high quality and upland roost exits are directly adjacent to woodland cover and this increased shelter may allow the bats to exploit further the abundance of insects at dusk and dawn. Therefore artificial lighting near roost exits should be avoided and tree and scrub cover close to the roost should be maintained and enhanced through planting. However it is important to maintain the roost entrance clear, an opening of 300 mm x 200 mm is recommended (Mitchell-Jones 1999), and to avoid excessive shading of the roost which may be detrimental to internal roost temperatures. Although presence of cover should reduce predation risk monitoring may be required to ensure bats are not at increased risk from sparrowhawks *Accipiter nisus*, which specialise in catching prey in physically cluttered environments (Duvergé 1996).

Foraging habitats

Broad-leaved and mixed woodland

Existing areas of mature broad-leaved and mixed woodland should be retained, particularly within 1 km of a maternity roost. A mixed age range may be of value early in the breeding season as younger trees may be in leaf earlier than mature

trees. To further maximise edge habitat woodland should contain rides and glades, managed without insecticides. Sheltered and sunny open space is of vital importance to many woodland invertebrates, as are wood margins (Kirby 2001). Therefore rides and glades should allow sufficient light to penetrate whilst maintaining sheltered conditions, for example by using curved ends or side scalloping. For invertebrates a well-structured ride or edge should show a gradation from low vegetation through to scrub and then trees. In small woodlands creation of new well-structured wood margins using scalloped edges or bays may be more appropriate than creating glades or rides.

Creation of woodlands should be encouraged. An enclosed area may be allowed to regenerate naturally or planting using species of local provenance should be undertaken. Even small woods (e.g. 0.3 ha) and copses have potential to be used by the species. Finally, old orchards should be retained and insecticide use restricted.

Coniferous woods

Coniferous woodland should contain rides and glades fringed with broad-leaved species and any streams or watercourses should be protected with a buffer strip and fringed with broad-leaved species. The edges of coniferous woodland should also be fringed with broad-leaved tree species. These broad-leaved zones should be protected from felling operations and would maintain connectivity during successive clearance and re-planting of crop trees. Where possible coniferous plantations should be replaced with deciduous trees gradually over a period of time, avoiding extensive clear-felling.

Pastures and other fields

Pasture fields were generally preferred over arable fields, with arable land used less than predicted from its availability. Therefore permanent pasture should be retained and encouraged within the vicinity of the roost. The structure of pasture fields appears to be important with those with 25 % or more associated tree cover

being preferred. Therefore the provision of treelines or field corner copses would be beneficial, assuming connectivity is also achieved.

Fields were significantly smaller in the high quality landscape with an average field size of just 0.75 ha. Reinstating former boundaries or sub-dividing fields should be encouraged. Such small fields are unlikely to be practical on a large scale for the majority of farms but many small-holdings and horse-grazed pastures in the lowland locality are currently bounded by fences. Provision of hedges with emergent trees could be practical in such situations.

Scathophagidae was one of the major prey categories in the diet, comprising 8 % frequency of the diet overall, and there is some evidence to suggest that it is observed significantly more than expected in the post-parturition diet. Therefore grazing may be of some importance and should be encouraged, particularly with cattle. The use of antihelminthic drugs in cattle and sheep to kill internal parasites is widespread and Coleoptera and higher Diptera are particularly sensitive to avermectin drug residues (Strong 1993, Strong et al. 1996). However sustained-release boluses are primarily used in first year grazing animals with a systemic used in second summer if they have not calved, thereby only a proportion of dung is affected. Until the likely impact of this on *R. hipposideros* has been evaluated further it is recommended that use of avermectins be avoided around maternity roosts. If this is not practical then it is recommended that first year grazing animals be grazed outside of the 1 km zone, or within pasture fields lacking associated tree cover or be treated with non-avermectin compounds.

Provision of buffer strips around pasture and arable fields is commonly recommended in agri-environment schemes. Although there are no data from the current study from which to assess whether these are of value to *R. hipposideros* they are likely to benefit invertebrate abundance and can protect bordering habitats from spray drift.

Hedgerows

Existing hedgerows should be retained as a priority. Their removal or degeneration into a gappy structure could be highly detrimental to a colony depending on the location. Gappy hedges should be either fenced to protect from grazing and encourage natural regeneration, or planted up to achieve a continuous structure.

Tall hedges, defined as 3 m or more in height with a canopy-like structure i.e. outgrown and bushy, should be protected and encouraged. Insect densities are typically greater nearer vertical landscape features (Lewis and Stephenson 1966, Verboom and Spoelstra 1999) and Wickramasinghe *et al.* (2003) found a significant correlation between the number of bat feeding buzzes and hedgerow height. Cessation of flailing on presently managed hedges would allow them to mature and obtain this structure. Periodic management would be required to retain a dense base, for example by hedge laying or coppicing, but this should be done strictly on rotation. Emergent standard trees should be encouraged either by allowing young saplings to grow on or by planting and would increase the overall tree cover of an area. Peng *et al.* (1992b) suggest that the emergent hedgerow tree plays a very important part in the life of flying insects. Where regular management is required, for example along roadsides where sightlines are required, then standard trees should be promoted. Traditionally, hedgerow trees would have occurred at much greater densities, for example 6.7 trees per acre of farmland in the mid-eighteenth century (Rackham 1990).

Hedgerows should be reinstated or new hedges planted along field boundaries currently comprising fencing. New hedges should be broad (2 m or more in width) to allow them to develop the tall, bushy, dense structure detailed above. However if this is not practical then the standard double row staggered planting should be undertaken. In both cases it is important to plant frequent standards along the length given the likely importance of broad-leaved tree cover.

Waterbodies

Natural features of waterbodies, such as pools and riffles, should be retained and encouraged to promote high insect diversity. Existing bankside trees should be retained and connectivity increased by planting or allowing natural regeneration by fencing off margins from grazing stock. However as excessive shading may reduce in-stream productivity, for example around riffles, planting should be evaluated on a site-by-site basis. Buffer strips along watercourses would reduce the risk of spray drift from agricultural fields. Agricultural run-off should also be avoided.

Rural settlements and farms

Existing night-roosts and alternative day roosts should be retained until we have a greater understanding of the impact their loss would have both on the individual(s) concerned and in terms of the cumulative effect on the maternity colony. When such roosts are threatened, for example due to proposed conversion to residential dwellings, mitigation may be required to retain the roost in part of the building or provide an alternative in close proximity. Additional roosts could be encouraged in structures such as modern garages and porches.

My study shows that broad-leaved tree cover within rural settlements provides foraging opportunities for *R. hipposideros.* House-holders could be encouraged to retain existing semi-mature and mature broad-leaved standards within gardens and to plant new trees, particularly within gardens on the edge of rural settlements adjacent to agricultural land.

Notwithstanding the value of rural settlements, urbanisation resulting in loss of habitat and fragmentation would be detrimental and should be avoided around maternity roosts. Although the analysis indicated the single-carriageway main roads in the lowland locality were not restricting dispersal around the roost, dual carriageways and motorways are likely to form a significant barrier to the species. Where *R. hipposideros* do cross such features a high mortality rate is likely to result.